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The combined effect of dispersal and chemical stress on the composition, diversity and productivity of marine micro-algae communities

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Jonathan De Raedt

The combined effect of dispersal and
chemical stress on the composition, diversity
and productivity of marine micro-algae
communities

Thesis submitted in fulfilment of the requirements for the degree of Doctor
(PhD) in Applied Biological Sciences

Thesis submitted in fulfilment of the requirements for the degree of Doctor
(PhD) in Sciences



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Voorwoord

Met dit boekje zet ik een punt achter 10 jaar boerekot. Het waren bijzonder mooie jaren tijdens dewelke ik heel wat heb geleerd en talrijke mensen heb ontmoet. Nochtans was de keuze voor een bio-ingenieursopleiding niet gemakkelijk. Ik heb immers maandenlang getwijfeld tussen de opleiding politieke (no kidding) en bio-ingenieurswetenschappen. Uiteindelijk koos ik, mede door toedoen van Yves en Francis, voor het laatste. Het bleek een goeie keuze want ik reken graag, en dat kon ik bij de bio-ingenieurs van harte doen. Ik bedenk me bovendien dat ik het gemis aan sociale wetenschappen heb proberen compenseren tijdens mijn doctoraat. Politieke wetenschappers onderzoeken immers interacties tussen mensen, en ik onderzocht interacties tussen algen. Dat is toch een beetje hetzelfde?

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List of Abbreviations

AIC	Akaike Information Criterion
ANOVA	Analysis Of Variance
DACT	<i>Dactyliosolen</i> sp., algae genus
EC_{50}	50% effect concentration
EU	European Union
f/2	Half the concentration of the 'f-medium' formulation by Guillard and Ryther
GC-MS	Gas chromatography-mass spectrometry
GLM	Generalized Linear Model
IUCN	International Union for Conservation of Nature and Natural Resources
LogLik	Log Likelihood
OD	<i>Odontella</i> sp., algae genus
sd	standard deviation

1

General introduction

1.1 A global decline in biodiversity

The earth is experiencing drastic changes in global biodiversity (Butchart et al. 2010, Barnosky et al. 2011, Dornelas et al. 2014, Pimm et al. 2014, Newbol et al. 2016, IUCN 2017). Today, the species extinction rate is estimated to be approximately 1000 times faster than the background extinction value (Pimm et al. 2014) and an increasing number of species is threatened by extinction (IUCN 2017). The global decline of biodiversity is mainly the result of human-induced environmental changes, such as climate change, changing nutrient cycles, habitat destruction, invasive species and the release of chemical stressors (Rockstrom et al. 2009, Butchart et al. 2010). Among these, habitat destruction is considered to be a main cause of species extinction (Pimm and Raven 2000). It includes the reduction, fragmentation, and degradation of habitats, often for the purpose of agriculture, mining or urban expansion. Habitat destruction does not only decrease the inhabitable area for organisms, it also declines the number of species in the remnant habitat patches by restricting movement and reducing genetic diversity (Lenore Fahring 2003, Ewers and Didham 2006). One factor that affects land degradation is the release of nutrients and anthropogenic chemicals such as metals, pesticides and polycyclic aromatic hydrocarbons. Those agents can impose serious threats to water security and biodiversity (Vörösmarty et al. 2010). In a continental risk assessment in Europe, organic chemicals were reported to be present at concentrations that likely exert acute lethal and chronic long-term effects on sensitive fish, invertebrate, and algae species in freshwater (Malaj et al. 2014).

While there is a general consensus that diversity is declining on a global scale, there is much debate about how the diversity of local communities evolves (Sax and Gaines 2003, Vellend et al. 2013, Dornelas et al. 2014, Gonzalez et al. 2016). Meta-analyses of temporal changes of local diversity indicate that diversity does not show an overall time-trend (Vellend et al. 2013, Dornelas et al. 2014), but that the way diversity changes over time has a high variability among discrete areas, running from negative to positive. For instance, succession experiments after a major disturbance as fire or severe storms often show increases of diversity over time, while areas that are affected by climate change show decreases of diversity (Vellend et al. 2013). Moreover, while most studies consider richness as a measure of diversity (e.g. Vellend et al. 2013, Dornelas et al. 2014), environmental change can also affect other measures of diversity, such as evenness, which describes how equal in numbers the species in a community are (box 1) (Hillebrand et al. 2008, Mensens et al. 2015). Last, environmental change does not necessarily change all diversity metrics. Analyses show a turnover in local species composition in time in many local communities, which indicates rather a substitution of taxa than a systematic loss (Dornelas et al. 2014). This turnover can be

caused by changing environmental conditions (De Laender et al. 2016), as well as by immigration of nonnative species (Dornelas et al. 2014). Moreover, environmental change can affect productivity without affecting diversity (De Laender et al. 2016, Spaak et al. 2017).

1.2 Local processes in isolated communities

1.2.1 Local drivers of coexistence and diversity

Organisms are not randomly distributed. The presence of a species depends on abiotic (temperature, resources...) and biotic factors (predation, facilitation, competition...), which determine a species' niche. The niche concept has many definitions, but in this thesis, I will use the definition of Chase and Leibold (2003): a niche of a species is made up of the requirement and impact niche. The requirement niche is made up of the environmental conditions that allows a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate. The impact niche consists of the set of per capita impacts that species have on those environmental conditions. For instance, species consume resources and thus decrease the resource level.

When species have a similar niche and thus compete for the same limiting resources, interspecific competition may result in the exclusion of less-competitive species (Tilman 1977). However, when niche differences are sufficiently large, coexistence is possible (Chesson 2000, Adler et al. 2007). By occupying different niches, species may limit their own population more than they limit the population of other species, which generates stronger interactions within (i.e. intraspecific interactions) than among (i.e. interspecific interactions) species. Therefore, when the abundance of a species increases, its per capita growth rate decreases compared to the per capita growth rate of the other species. Therefore, niche differences can lead to coexistence, also named stabilizing mechanisms (Fig. 1.1) (Chesson 2000). However, stabilizing mechanisms alone do not ensure stable coexistence as coexistence also depends on the fitness differences among species (Fig. 1.1). When species have a nearly identical fitness, species turnover is low and mainly caused by stochastic extinctions and speciation rather than the selection of the competitive strongest species (Hubbell 2001). Low fitness differences that facilitate coexistence are named equalizing mechanisms (Chesson 2000). When fitness differences are large, strong stabilizing effects are needed to insure coexistence. In contrast, when stabilizing effects are low, low fitness differences can generate coexistence.

Box 1. Measuring biodiversity

The word biodiversity is a contraction of *biological diversity*, and is a measure of the complexity (amount and variability) at different levels of biological organization (Purvis and Hector 2000). It can be measured at different levels, going from genes to species and ecosystems. In this dissertation, I focus on species (taxonomic) diversity. Taxonomic diversity is composed of two components: species richness and species evenness. The first is the quantification of the number of species, which is the commonly used approach. The second is a measure of how equal the species abundances are. Diversity can be calculated using several metrics that contain both components (Whittaker 1972). Of these metrics, the Simpson diversity and Shannon-Wiener index are most commonly used. Diversity can be measured at several spatial scales: alpha or local diversity is defined as the diversity at the habitat-patch-level, whereas gamma or regional diversity is defined as the diversity at the landscape level. Beta-diversity expresses the diversity among habitat patches. Beta-diversity can be calculated using the additive definition of diversity H (Jost 2006):

$$H_{\beta} = H_{\gamma} - H_{\alpha} \quad (\text{Eq. 1.1})$$

Beta-diversity can also be calculated using dissimilarity indices, such as the Bray-Curtis dissimilarity index (Bray and Curtis 1957) and the Jaccard's index (Jaccard 1912).

1.2.2 The effect of stress on composition and diversity

A special case of abiotic factors that influence community composition are agents that expose organisms to stress. Stress can be defined as a negative physiological or functional response towards the environment when the environment exceeds its range of normal variation (Barrett et al. 1976) (Box 2). There are many types of environmental stress, such as drought, heat and chemical stress. Chemical stress is the result of the release of chemical stressors such as pesticides and heavy metals in the environment, mainly through anthropogenic activities. The ecological risk assessment of chemicals aims to determine the exposure of organisms by chemicals in the environment and to assess the effects of chemicals on living organisms on several levels of biological organization from cells to species and ecosystems.

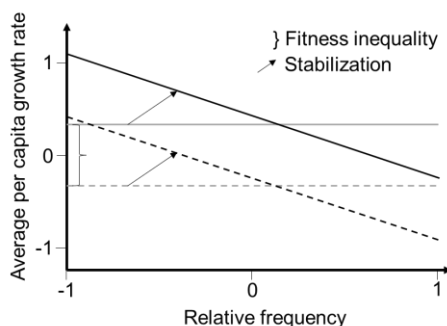


Fig. 1.1. Representation of equalizing and stabilizing mechanisms using two species (full and dashed line). The difference in per capita growth rate in the absence of stabilization is the fitness difference (grey lines). The smaller the difference is fitness, the higher the equalizing mechanisms are. A negative slope of the relationship between per capita population growth rate and the species' relative frequency (black lines) represent the degree of stabilization. The stronger the slope, the stronger the stabilizing mechanisms. Redrawn from Adler et al. (2007).

Stress affects species directly by decreasing their birth or increasing their death rates. Environmental change may generate a variety of environmental responses among species as species occupy different niches along an environmental gradient. Therefore, environmental change can decrease the performance of some species (exposing those species to stress), while it may increase the performance of others (Woodward et al. 2010). Moreover, environmental niches may be smaller for some species than for others. Therefore, environmental change can induce a strong stress response in some species, while it may only generate a weak response in others (Chase and Leibold 2003, Bolnick et al. 2010, De Laender et al. 2016).

Next to direct effects, stress may also have indirect effects through species interactions. According to the stress-gradient hypothesis, the number of facilitative interactions increases across gradients of physical stress (Grime 1973, Maestre et al. 2009). For instance, in water-limited environments, plants can increase water availability by hydraulic lifting or by increasing water availability in the top soil by shading surface areas. However, the stress-gradient hypothesis is often criticized (Chesson and Huntly 1997). Studies have shown that extreme stress can decrease or cease facilitative effects (Michalet et al. 2006) and that the transition from competition to facilitation depends on the species identity (Choler et al. 2001) and the stress type (Kawai and Tokeshi 2007, Maestre et al. 2009) that are tested.

Environmental stress decreases diversity when stress-sensitive species are not able to persist locally or when environmental stress reduces the abundance of a locally subdominant species

more than the abundance of the dominant species (Odum 1985, Johnston and Roberts 2009). However, environmental stress can also increase diversity by reducing the abundance of a locally competitive dominant species more than that of the subdominant species (Odum 1985, De Laender et al. 2016).

1.2.3 The relationship between diversity and productivity

A vast number of studies have demonstrated that richness increases ecosystem functions such as productivity (Naeem et al. 1994, Tilman and Downing 1994, Tilman et al. 1997, Loreau et al. 2001, Hooper et al. 2005, Cardinale et al. 2013a). Biodiversity affects ecosystem functioning because of two mechanisms: complementarity and selection effects (Loreau and Hector 2001). Complementarity effects occur because of niche differentiation and facilitative interactions. First, when species differ in their niche, competition between organisms of different species is lower than between organisms of the same species. Niche differentiation therefore reduces the strength of competition, increasing productivity. While niche differentiation is the avoidance of competitive (negative) interactions, facilitative interactions increase positive interactions among species (e.g. flower-pollinator interactions). Under both niche differentiation and facilitative interactions, high-diverse systems can sustain a higher number of individuals and hence have a higher productivity than low-diverse systems. Selection effects occur when productivity is driven by high functional contributions of species with particular traits. Under selection effects, the species with those particular traits will contribute most to productivity, while the species that do not possess those traits will contribute less. Selection effects are likely to generate local extinctions of less-productive species, decreasing diversity. However, a high initial diversity increases selection effects because of a sampling effect i.e. a high initial diversity increases the probability that a very productive species is locally present. There is some evidence that selection effects increase under stress (Baert et al. 2016a). A high diversity increases the probability that a stress-tolerant species is present which can replace stress-sensitive species. As such, diversity may provide insurance against a negative effect of stress on productivity (Yachi and Loreau 1999, Fernandes et al. 2011, Steudel et al. 2012, Baert et al. 2016a).

The strength of selection and complementarity effects depends on which species are initially present in a community (Huston 1997). However classic diversity-productivity studies cannot explain why certain species are initially present and which factors may determine initial diversity. Expanding the scope to how local processes interact with regional processes is therefore a logical next step to understand how diversity affects the productivity of communities (Mouquet and Loreau 2003, Loreau et al. 2003a, Gonzalez and Loreau 2009, Leibold et al. 2017).

1.3 Effect of regional processes on species composition

Organisms can interact at different spatial scales (Robert and Wilson 1967, Levin 1992, Chase and Leibold 2002, Leibold et al. 2004). A patch is an area of the habitat that can contain a local population or community (Leibold et al. 2004). A region is a larger area of the habitat, containing multiple patches and being capable of supporting a set of local populations or communities (Leibold et al. 2004). There are multiple ways in which such a region can be structured. One way is the classic mainland-island system, where local dynamics only occur within the islands (Robert and Wilson 1967). Those local dynamics can drive the species on the islands to extinction. However, local diversity is influenced, and potentially saved, by immigration from the mainland. Another way is the Levins metapopulation system, which is a set of identical local populations with finite and equal probabilities of extinction and immigration (Levins 1969). An extension of this system is the metacommunity system (Wilson 1992, Leibold et al. 2004). A metacommunity is a set of local communities that are linked by dispersal of multiple potentially interacting species (Leibold et al. 2004). The way regional processes change local processes in metacommunities depends on connectivity (dispersal), the regional species pool, disturbance and environmental heterogeneity and variability (Leibold et al. 2017) (box 2). Those processes determine which community assembly processes will regulate diversity and productivity on a local (community) and a regional (metacommunity, landscape) scale (Fig. 1.1).

1.3.1 Community assembly mechanism 1: neutral model

According to the neutral model, the environment is completely homogeneous and all species have identical traits (Fig. 1.2) (Hubbell 2001). Processes such as birth and death are random processes, which generate random species extinctions. Diversity is maintained as local extinctions are compensated by the dispersal of species from other communities and by speciation (Hubbell 2001, Vellend 2010). The neutral model is valuable as it can be considered a null hypothesis, or describe dynamics where fitness differences among species are small and transient dynamics are long-lived (Leibold et al. 2004, Vellend et al. 2014).

Box 2. Factors that determine the community assembly processes

Dispersal is the movement and incorporation of organisms between populations and communities (Ronce O. 2007, Edelaar and Bolnick 2012). It contains several stages: departure, transfer and settlement. Dispersal can be active or passive (Edelaar and Bolnick 2012). Dispersal shows a high interspecific and intraspecific variability (Baguette et al. 2013, Cote et al. 2016, Bonte and Dahiriel 2017) and might be condition-dependent (Edelaar and Bolnick 2012, Fronhofer et al. 2015a, 2015b). In this dissertation, I use dispersal rate as the number or proportion of organisms that move from one community to another.

Connectivity is the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993). Connectivity encompasses structural connectivity (the physical arrangements of patches) and functional connectivity (the movement of individuals among patches) (Brooks 2003, Baguette et al. 2013). The degree to which a landscape is connected determines the amount of dispersal among patches. In this dissertation, I use connectivity as the number of connections among the patches of a landscape.

The regional species pool is the set of species in a region that could potentially colonize and establish within a community (Lessard et al. 2012). The region is defined as a large area containing multiple patches and is capable of supporting a metacommunity (Leibold et al. 2004). In reality, it is an area that is intermediate in extent between the entire globe and small study plots (Sax and Gaines 2003), such as a stream, drainage basin or an ecoregion (Heino et al. 2015). The identity of the species in the species pool will determine how communities will interact with e.g. environmental conditions (Lessard et al. 2012, Fukami 2015).

Environmental heterogeneity encompasses different kinds of spatial heterogeneity, complexity, diversity, structure, or variability in the environment (Stein and Kreft 2015). Environmental heterogeneity contains biotic and abiotic components such as land cover, vegetation, climate, soil, and topography. A high environmental heterogeneity is generally expected to generate a high regional diversity because of an increase of the available niche space (Chesson and Warner 1981, Hortal et al. 2009, Stein et al. 2014).

Disturbance is generally described as the total or partial disruption of biomass (Grime 1979). It is a relatively discrete event in time that is characterized by a frequency, intensity, and severity outside a predictable range, and that disrupts an ecosystem, community, or population and changes resources or the physical environment (Resh et

al. 1988). Because of disturbances, communities depart from their steady state and enter the exponential growth rate (Battisti et al. 2016).

Stress can be defined as the reduction of the biomass growth rate (Grime 1979). More general, it is a negative physiological or functional response towards the environment when the environment exceeds its range of normal variation (Barrett et al. 1976). Stress is a species-specific response as environmental stressors, such as chemicals or drought might severely stress some species, while not affecting other species (Van Straalen 2003, De Laender et al. 2016).

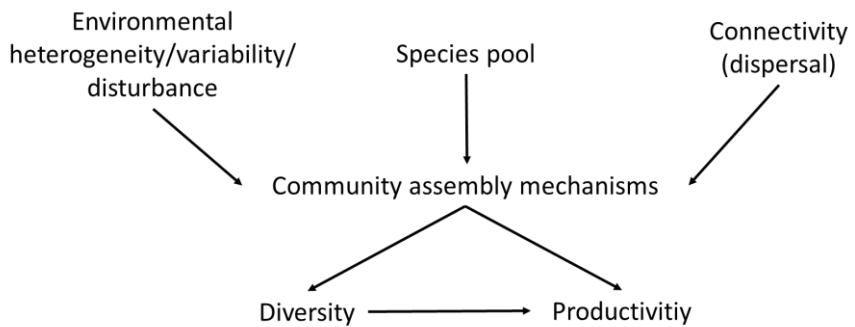


Fig. 1.2. The effect of diversity on productivity according to the metacommunity framework (Leibold et al. 2004, 2017). Metacommunity assembly processes are influenced by the species pool, the environment and connectivity and influence diversity. Species pool, environmental heterogeneity and connectivity can also directly influence productivity, but these relations are not shown as they are usually not directly considered within metacommunity theory. Figure after Leibold et al. (2017).

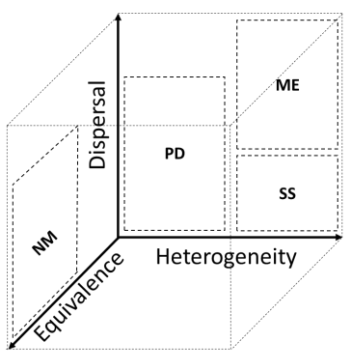


Fig. 1.3. The area of the four metacommunity assembly mechanisms where they are applicable. The mechanisms depend on environmental heterogeneity, fitness equivalence and dispersal rate. Abbreviations: NM, neutral model; PD patch-dynamics; SS, species sorting; ME, mass effects. Redrawn from Logue et al. (2011).

1.3.2 Community assembly mechanism 2: patch-dynamics

According to the patch-dynamic perspective, the environment is completely homogeneous and species are affected by local stochastic and deterministic extinctions that are counteracted by dispersal (Fig. 1.2) (Leibold et al. 2004). Coexistence is possible under a competition-colonization trade-off, in which some species colonize empty patches more efficiently, while others are better competitors and can locally outcompete the best colonizer (Levins and Culver 1971, Tilman 1994, Livingston et al. 2012). The trade-off between the species' colonizing and competitive ability reduces the ratio of interspecific to intraspecific competition and allows coexistence without environmental heterogeneity among patches (Amarasekare 2003). However, when the difference in dispersal rate is low, the best competitor will exclude the best colonizer. Likewise, when the difference in dispersal rate is too high, the best colonizer will exclude the best competitor (Livingston et al. 2012). An important feature needed to permit coexistence is that disturbance, such as habitat destruction, removes better competitors from local patches, opening new available patches for the better colonizers (Nee and May 1992). The existence of a competition-colonization trade-off has been found for some species combinations (Mouquet et al. 2004, Cadotte et al. 2006b), but not for many other species combinations (Yu and Wilson 2001, Jakobsson and Eriksson 2003, Limberger and Wickham 2011).

1.3.3 Community assembly mechanism 3: species sorting

The species sorting mechanism presumes a spatially heterogeneous environment, in which species sort among patches according to their performance and competitive abilities under local environmental conditions (Fig. 1.2) (Tilman 1982, Chase and Leibold 2003, Leibold et al. 2004, 2017). Optimal species sorting is achieved when each patch contains the species from the regional species pool that are best adapted to the local environmental conditions. Therefore, there is a strong relationship between the variability in composition and the variability in environmental conditions among patches (Cottenie 2005, Langenheder et al. 2012, Soininen 2014, Leibold et al. 2017).

There are at least three factors that can avoid the most competitive species to be present in its optimal patch. First, under dispersal limitation, dispersal rates can be too low to achieve optimal species sorting (Cornell and Lawton 1992, Tilman 1994, Shurin 2000). Dispersal limitation occurs when colonization or extinction rates are smaller than the rates of environmental changes, which reduces the propensity for species to find their favored environmental conditions (Germain et al. 2017, Leibold et al. 2017). Therefore, communities are dominated by subdominant species that can only persist when the dominant species is not present.

Second, historical processes can influence community assembly. The way species affect each other may depend on the order and timing in which species arrive in a local community. This effect of timing on community assembly is also referred to as priority effects (Chase 2003, Fukami 2015). By influencing community assembly, priority effects can lead to different community compositions and functioning among patches, although those patches may have identical environmental conditions (Shulman et al. 1983, Chase 2003, Zhang and Zhang 2007, Tan et al. 2012, Vellend et al. 2014). The different compositions that are generated by priority effects are not necessarily stable, but may also be transient (Fukami 2015). The mechanisms that generate priority effects are discussed in box 3.

Third, dispersal rates can be too high, which leads to mass effects.

1.3.4. Community assembly mechanism 4: Mass effects

The mass effect paradigm presumes a spatially heterogeneous environment in which species are moved from patches where they have a high growth rate and perform well, to patches where they have a low growth rate and perform worse (Fig. 1.2) (Loreau and Mouquet 1999, Amarasekare and Nisbet 2001, Mouquet and Loreau 2003). As a result, a species has a higher loss rate in the source community and a higher birth rate in the sink community than in isolated conditions. Mass effects occur at high dispersal rates, when dispersal prevails over local community dynamics such as competitive exclusion (Logue et al. 2011).

1.4 The effect of dispersal on diversity and productivity

In the previous paragraph, I discussed that dispersal can change local and regional coexistence through four different assembly mechanisms. By changing coexistence, dispersal also potentially affects diversity and productivity (Fig. 1.1), which it can do in various ways. Grainger and Gilbert (2016) reported in a recent meta-analysis a high variation in relationships between dispersal and diversity. Most studies that were included in the meta-analysis reported a positive relationship between dispersal and local (alpha) diversity (measured as richness). Other studies found negative, hump-shaped or no significant relationships. Studies were more consistent about how dispersal affects among-community (beta) diversity, reporting mainly negative relationships. In contrast, studies showed a high variation in how dispersal affects regional (gamma) diversity. Most studies reported no significant effect of dispersal on regional diversity, while others found a positive or negative effect. Most studies that were included into the analysis used richness as a measure of diversity, while studies about evenness are largely lacking (Hillebrand et al. 2008). Nevertheless, there is experimental evidence that dispersal might affect evenness more than richness because local or regional processes often rather

change the relative abundance of certain species than driving species to extinction (Matthiessen et al. 2010a, Limberger et al. 2014, Mensens et al. 2015).

Dispersal can also affect productivity. Although Loreau et al. (2003b) already showed theoretically that dispersal can affect productivity, experimental evidence is not conclusive. Moreover, the experimental studies that investigated the relationship between dispersal and productivity show a high variation in possible relationships. Positive (e.g. Thompson and Shurin 2012, Steiner 2014), hump-shaped (e.g. Matthiessen and Hillebrand 2006, Howeth and Leibold 2010) and negative (e.g. Eggers et al. 2012, de Boer et al. 2014) relationships between dispersal and local and regional productivity have been found. A high variety in dispersal effects on diversity and productivity is not surprising, as the effect of dispersal on diversity and productivity depends on many factors such as environmental heterogeneity, material fluxes and network structure.

1.4.1. The effect of dispersal on diversity

When environmental conditions are equal in all communities, the environment is homogeneous. In a homogeneous environment, species compositions among patches can differ because of stochastic extinctions. While species get locally extinct, dispersal introduces new species and thereby increases local diversity (i.e. neutral model, Leibold et al. 2004). However, in many experiments, differences in composition in homogeneous environments through stochastic dynamics are weak and dispersal hence does not affect diversity or productivity (Matthiessen et al. 2010a, Limberger et al. 2014, Guelzow et al. 2014).

Under the patch-dynamic mechanism, competition-colonization trade-offs can affect diversity. A competition-colonization trade-off generates the highest diversity at intermediate dispersal rates (Livingston et al. 2012). When dispersal is too low, the best competitor hardly moves among patches, and the best colonizer is the dominant species. However, when dispersal is too high, the difference in the colonizing ability decreases and the best competitor then regionally excludes the best colonizer.

An important factor that can influence how dispersal affects diversity in homogeneous landscapes is if the starting communities are heterogeneous (i.e. have a different composition). Under such conditions, species that are initially present may facilitate or inhibit the colonization of later-arriving species (Matthiessen and Hillebrand 2006, Fukami 2015). Moreover, increasing dispersal can enable species to colonize new patches, increasing diversity (Gonzalez et al. 1998), while high dispersal rates can enable a dominant competitor to reach all patches, decreasing diversity (Cadotte and Fukami 2005, Cadotte 2006). Therefore, heterogeneous starting communities might increase the probability to find hump-shaped relationships between dispersal and diversity (Grainger and Gilbert 2016).

Box 3. Priority effects.

Priority effects are caused by **two mechanisms**: niche preemption and niche modification.

Niche preemption inhibits the colonization of later-arriving species because their reproduction and survival rates were reduced by a low resource availability. Resource availability was low because resources were consumed by the early-arriving species (Fukami 2015). Niche preemption is stronger when species have a similar resource use, such as algae (Zhang and Zhang 2007) or amphipods (Little and Altermatt 2018) or when they have a similar fitness, which acts as an equalizing mechanism (Chesson 2000). Without niche preemption, the order of arrival would not be important, and species sorting effects would create communities that are dominated by the same species (Leibold et al. 2004). Because niche preemption is based on equalizing mechanisms, it generates no stable but only transient states (Adler et al. 2007, Fukami 2015).

Niche modification inhibits the colonization of late-arriving species or changes the identity of the late-arriving species because early-arriving species modified the environment. (Fukami 2015). For instance, early arriving species can change the soil conditions by bioturbation, creating a niche for other sea organisms (Meysman et al. 2006) or plants (Fukami and Nakajima 2011). Niche modification can lead to alternative stable (Pertraitis 2009), as well as transient states (Fukami and Nakajima 2013).

Priority effects are promoted by a number of **local and regional factors**.

First, priority effects are promoted by a **rapid growth of the early-arriving species** (Fukami 2015). A high growth rate assures that the habitat is substantially preempted or modified before the late-arriving species arrive. The growth rate must be considered relative to the dispersal rate. The higher the dispersal rate, the less time the early-arriving colonizers have to preempt or modify the niche, so the higher their growth rate must be (Chase 2003, Fukami 2005). Priority effects are thus facilitated when growth rates increase, for instance through a smaller patch size, which allows species to reach their carrying capacity earlier (Fukami 2004) or through a low environmental variability which keeps growth rates constant (Tucker and Fukami 2014). In contrast, growth rates decrease when communities are stressed. For instance, recurrent disturbances are shown to decrease priority effects (Chase 2003, Symons and Arnott 2014).

Second, the higher the **number of species in the species pool**, the more species there are to fill a certain niche, which increases the possibility for priority effects (Law and

Morton 1996). However, when only a few species are able to persist in a local patch, for instance through stress, the possibility for priority effects decreases (Chase 2003).

Third, **the traits of the species** are important (Tan et al. 2012, Fukami 2015). For instance, priority effects are expected to be high when resource overlap is high. Moreover, dispersal rates should be similar, increasing the variability in arrival order among patches.

Fourth, there should be a **decoupling of the species from local dynamics** (Fukami 2015). When all communities are connected, such as in the metacommunity perspective of Leibold et al. (2004), all communities are homogenized when dispersal is high and will likely obtain the most frequent community composition (Chase 2003). In a mainland-island system, the species composition of the mainland is not influenced by local dynamics (Robert and Wilson 1967). All species are thus able to invade the island, increasing the possibility for priority effects.

Different environmental conditions among patches create heterogeneous landscapes where patches hold different communities by maintaining the species that are best adapted to the local conditions. In empirical studies, environmental heterogeneity is generally created by varying disturbance intensity (Matthiessen et al. 2010b, Altermatt et al. 2011b, Carrara et al. 2012), resource availability (Forbes and Chase 2002, Davies et al. 2009, Souffreau et al. 2014), temperature (Eggers et al. 2012, Limberger et al. 2014, de Boer et al. 2014) or light intensity (Eggers et al. 2012, de Boer et al. 2014, Guelzow et al. 2014) among local patches. Applying disturbances differs from the others factors as it does not affect species randomly towards their contribution to ecosystem functioning. Indeed, as disturbance is mostly applied by removing a fixed proportion of a community, it affects the high-productive species most. In contrast, the effect of manipulating resource availability, temperature or light intensity depends on how species respond to the changing environment conditions. Although patch dynamics, neutral dynamics, species-sorting effects and mass effects can occur together, the last two are generally considered to be the main driving mechanisms of diversity in heterogeneous landscapes.

When dispersal increases, an increasing number of species can colonize a local patch (Shurin 2000). Low dispersal can generate species sorting, enabling species to track suitable patches. Species sorting may generate several effects on local diversity. First, dispersal can increase diversity when it adds species that are good competitors under the local environmental conditions. Second, dispersal might have no effect on diversity when the addition of a good local competitor induces the exclusion of a poor resident competitor. Last, dispersal can

decrease diversity when it introduces a competitive dominant species that excludes most of the local subdominant species (Leibold et al. 2017). Dispersal may also generate several effects on among-community diversity. Dispersal may decrease beta-diversity as species can reach more patches (Bender et al. 2017). In contrast, optimal species sorting increases beta-diversity when each patch is dominated by a different species (Gianuca et al. 2016, Leibold et al. 2017).

Increasing dispersal may induce mass effects. Under mass effects, dispersal is expected to show a hump-shaped relationship with local richness (Fig. 1.3) (Mouquet and Loreau 2003, Loreau et al. 2003a). When dispersal is absent, local diversity is low as each community consists of the species that are best adapted to the local environmental conditions. When dispersal increases, it may introduce species to patches where they could not survive without dispersal. When dispersal is high, dispersal decreases local diversity as it distributes a regional dominant competitor that excludes the regional subdominant competitors. However, many studies that manipulate dispersal under mass effects did not find any effect of dispersal on local richness (Matthiessen et al. 2010a, Altermatt et al. 2011a, Eggers et al. 2012, Limberger et al. 2014). However, some of these studies found a negative effect of dispersal on local evenness (Matthiessen et al. 2010a, Eggers et al. 2012). This negative effect occurs when dispersal promotes a regional dominant species as predicted by theory.

As dispersal homogenizes composition under mass effects, it is expected to decrease beta-diversity (Mouquet and Loreau 2003), which has been confirmed in several experiments (Matthiessen et al. 2010a, Carrara et al. 2012, Eggers et al. 2012). Last, high dispersal rates are also predicted to decrease regional diversity (Mouquet and Loreau 2003). Only a few studies found a negative relationship between dispersal and regional diversity (e.g. Matthiessen et al. 2010a), while a majority of studies did not find a significant relationship between dispersal and regional diversity (e.g. Eggers et al. 2012, Limberger et al. 2014).

1.4.2 The effect of dispersal on productivity

Dispersal can increase productivity by adding new species to local communities. When dispersal adds new species, complementarity effects and selection effects may increase (Matthiessen and Hillebrand 2006, Leibold et al. 2017). Complementarity effects increase productivity through niche partitioning. How selection effects change productivity depends on the identity of the competitive dominant species (Loreau and Hector 2001, Fox 2005). When the dominant species is also most productive, selection effects increase productivity. However, selection effects may also be negative and decrease productivity.

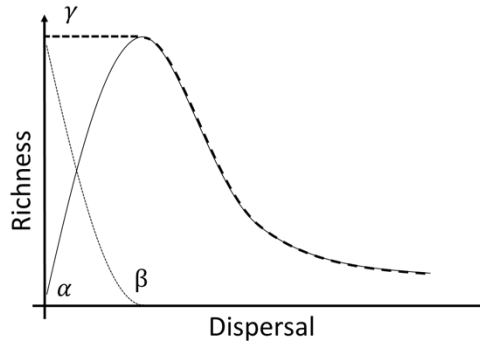


Fig. 1.4. Predicted relationships between dispersal and richness according to the model simulation of Mouquet and Loreau (2003). The relationships are the result of dispersal-induced mass effects. The relationship between dispersal and local (α) richness was predicted to be hump-shaped because low dispersal initially supplies new species while high dispersal generates extinctions of regionally subdominant species. Because of the regional exclusion of subdominant species at high dispersal, the relationship between dispersal and regional (γ) diversity was found to be negative. Finally, the relationship between dispersal and among-community (β) diversity was found to be negative because of an increasing homogenization.

When environmental conditions fluctuate through time, dispersal can increase compensatory dynamics by increasing local diversity. By increasing compensatory dynamics, dispersal increases productivity, providing spatial insurance under changing environmental conditions (Loreau et al. 2003a, Brown et al. 2016). Increasing compensatory dynamics have been empirically found in communities where asynchronous pH fluctuations were applied (Steiner et al. 2011) and in communities under salt stress (Thompson and Shurin 2012). Dispersal may also increase productivity by generating a spatial averaging effect which means that a regional dominant competitor will always find a patch where it can perform well and averages out environmental variations across the various local patches (Loreau et al. 2003a). For instance, spatial averaging has been found in metacommunities under a pulsed inflow of nutrients (Smeti et al. 2016).

Dispersal can also decrease productivity. Under mass effects, dispersal is predicted to decrease biomass because it moves organisms to patches in which they are less productive and replaces those organisms with organisms that are less productive (Mouquet and Loreau 2003). However, empirical evidence for this is limited (Leibold et al. 2017). Negative effects of dispersal on local and regional productivity have mainly been confirmed at high dispersal rates (Howeth and Leibold 2010a, Lindström and Östman 2011), but also at low dispersal rates for algae metacommunities (Eggers et al. 2012, de Boer et al. 2014).

1.4.3 Material fluxes

Not only organisms, but also materials and energy can move across a landscape (Loreau et al. 2003b, Massol et al. 2011, 2017). Systems in which dispersal and material fluxes are investigated together are named metaecosystems. By changing the environmental conditions, material fluxes are predicted to change the relationship between dispersal and diversity (Loreau et al. 2003b, Massol et al. 2011, 2017). Haegeman and Loreau (2014) found a resource flux to change the relationship between dispersal and local diversity from positive to hump-shaped because the combination of dispersal and a resource flux facilitated a regional dominant competitor to exclude other species. A resource flux is also shown to change productivity. For instance, a resource flux between an autotrophic and heterotrophic patch can increase the productivity of both communities (Harvey et al. 2016, Gounand et al. 2017). However, empirical studies that investigate the combined effect of dispersal and material fluxes on diversity and productivity are lacking (Massol et al. 2017).

1.4.4 Network structure

Most studies that investigate the effect of dispersal on diversity and productivity in landscapes only contain two or three patches (e.g. Matthiessen et al. 2010a, Pedruski and Arnott 2011, Eggers et al. 2012, Limberger et al. 2014, Souffreau et al. 2014). However, real landscapes are spatially extended, containing multiple patches (Davies et al. 2009, Carrara et al. 2012, 2014). In such landscapes, the position of the patch within the network is demonstrated to influence the diversity of the patch (Carrara et al. 2012, Seymour et al. 2015). Patches that occupy a central position in a network are shown to have the highest diversity as they are more strongly connected to other patches than peripheral patches (Carrara et al. 2014). Moreover, in spatially extended landscapes, also the direction of dispersal is an important determinant of diversity. For instance, in patches that were affected by random disturbances, Altermatt et al. (2011b) found that dispersal in one direction decreased local richness more than when dispersal occurred in all directions. This effect was stronger when dispersal was biased away from the disturbed patches. Spatially-extended networks are a better representation of real landscapes than simple two-or three patch metacommunities. However, the effect of dispersal on diversity or productivity has hardly been investigated in such landscapes (Grainger and Gilbert 2016).

1.5 Rationale, research objectives and thesis outline

Environmental change is predicted to be a main driver of alterations in the composition of communities, influencing community diversity and productivity (Cardinale et al. 2012, Pimm et al. 2014, Baert et al. 2016a, De Laender et al. 2016, Spaak et al. 2017). The way

environmental change affects diversity and productivity depends on both local (i.e. species responses and competitive interactions) and regional processes (Robert and Wilson 1967, Mouquet and Loreau 2003, Leibold et al. 2004). However, how environmental change and dispersal combine in affecting diversity and productivity is still poorly understood. Several studies have investigated how dispersal affects diversity or productivity when environmental heterogeneity creates different compositions among communities (Grainger and Gilbert 2016). The extent to which environmental change creates different compositions depends on the strength of environmental heterogeneity and the species responses to environmental change. However, the magnitude of compositional changes that are needed to create dispersal effects on diversity and productivity is still poorly understood. Moreover, environmental change may not only generate differences in composition by generating species turnovers, but also alter population sizes. How changes in population size alter dispersal effects on diversity and productivity has hardly been examined until now. An important group of environmental-change drivers that affect both the composition and population size of communities are environmental stressors such as chemicals. In this dissertation, I investigate how chemical stress and dispersal combine in affecting diversity and productivity. I formulate four research questions, which are each addressed in a different chapter. The experimental set-ups that were applied to investigate the research questions are represented in Fig. 1.4.

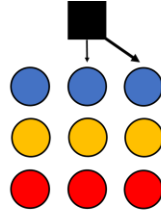
Environmental stress induces shifts in community composition and reduces productivity by decreasing the growth rate of species. Dispersal may introduce stress tolerant species, changing composition and compensating for the stressor-induced productivity loss (Loreau et al. 2003a). However, the colonization of new species might be hindered by priority effects (Chase 2003, Fukami 2015). Until now, it has not been investigated how chemical stress and dispersal combine in affecting community assembly and how this affects the diversity and productivity of communities. In **chapter 2**, I therefore address the question: “*How does dispersal affect the assembly, diversity and productivity of communities at different levels of chemical stress?*”. I performed a laboratory microcosm experiment in which I exposed marine micro-algae communities to chemical stress and dispersal using a full-factorial design. For the experiment (as well for the experiments in chapters 4 and 5), I used marine micro-algae communities of the class *Bacillariophyceae* (diatoms). These micro-algae were sampled in the North Sea where they form the basis of the marine food web (Mommaerts 1973, Gypens et al. 2007). Under laboratory conditions micro-algae communities are characterized by high competitive interactions, often resulting in the dominance of a few algae species (Giller et al. 2004, Mensens et al. 2015, Baert et al. 2016a). Micro-algae have a high growth rate, which enables studying multiple generations in less than a month. Moreover, they have a high

interspecific variation in response towards herbicides (Mensens et al. 2015). In chapter 2, I exposed the micro-algae communities to chemical stress using the herbicide atrazine, which is a triazine herbicide that targets photosynthesis. While its application has been forbidden in Europe since 2004 (European Commission 2004), it is still a widely used pesticide in many other areas. For instance, in the US, concentrations of atrazine in exposed watersheds typically vary between 1 and 3 $\mu\text{g/l}$ (Mahler et al. 2017), although also concentration peak concentrations of 100 $\mu\text{g/l}$ have been recorded (Graymore et al. 2001). Atrazine has a high half-life value (several weeks or months, Salomon et al. (2010)), which facilitates studying the effect of atrazine while keeping its concentration relatively constant over time. Dispersal was performed according to a mainland-island design (Robert and Wilson 1967). I measured the species abundances throughout the experiment and calculated the diversity, productivity and the abundance of the initial species as a measure for the priority effect.

In chapter 2, I introduced species to communities without allowing them to emigrate from those communities. Moreover, the identity of the introduced species did not emerge from community processes. In reality, species move among communities, and the identity and the number of organisms that immigrate depend on the composition of the source communities. Stress heterogeneity is an important factor that generates different compositions among communities and as such influences the relationship between dispersal and diversity. The extent to which stress heterogeneity creates different compositions among communities, depends on the interspecific variation in stress response. Moreover, differences in composition may also be due to heterogeneous initial communities. As such, heterogeneous initial communities may generate different dispersal effects on diversity than homogeneous initial communities. In **chapter 3**, I therefore address the question: *“How does the relationship between dispersal and local richness change at different magnitudes of stress heterogeneity?”* I used a theoretical model to simulate the relationship between dispersal and diversity in metacommunities where stress intensity varied among two communities. Using a full factorial design, I investigated how stress heterogeneity, interspecific variation in stress response and the composition of the initial communities (homogeneous versus heterogeneous) affected the relationship between dispersal and diversity.

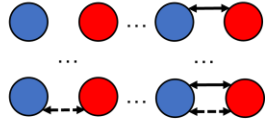
Chapter 2.

- Dispersal not dependent of local dynamics
- 3 stress levels x 3 dispersal levels



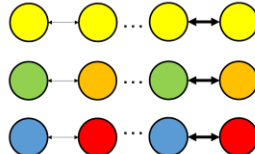
Chapter 4.

- Dispersal depends on local dynamics
- 2 stress levels x 5 dispersal rates x 4 stressor flux levels



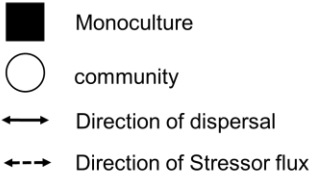
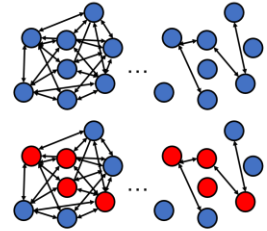
Chapter 3.

- Dispersal depends on local dynamics
- 6 stress levels x 7 dispersal rates



Chapter 5.

- Dispersal depends on local dynamics
- 2 stress levels x 6 connectivity levels



No stress  High stress

Fig. 1.5. Experimental set-up in each research chapter. Each colored circle represents a patch (i.e. an algae community). Colors represent the different stressor levels (from low to high: blue, green, yellow, orange and red). A thicker line represents a higher dispersal rate. In chapter 2, algae were moved at a fixed density (3 levels) from the monocultures to the communities that initially contained 4 algae and that were exposed to three levels of atrazine. In reality, the number of organisms that disperses is often the result of interactions in the community from which the organisms emigrate. Therefore, in chapter 3, I moved organisms between two communities that had a different stress intensity. While in chapter 2 and 3 only organisms were dispersed, also materials such as chemical stressors can move among communities. In chapter 4, I therefore crossed 5 dispersal levels with 4 stressor flux levels in two-patch metacommunities. Finally, in contrast to the two-patch metacommunities that were used in chapters 3 and 4, organisms were dispersed in chapter 5 between patches in spatially extended landscapes. 8-patch landscapes were hence exposed to 2 levels of atrazine and algae were dispersed between patches according to different connectivity schemes.

In chapters 2 and 3, the dispersal of organisms was the only flux that was considered. Many landscapes, however, are not only characterized by fluxes of organisms, but also by fluxes of materials, such resources and chemical stressors (Massol et al. 2017), which can introduce temporal changes of stressors. Although such fluxes have been theoretically shown to change the relationship between dispersal and diversity (Haegeman and Loreau 2014), only one experimental study so far has combined dispersal and a resource flux (Harvey et al. 2016). In

chapter 4, I therefore address the question *“How does a stressor flux alter the relationship between beta-diversity and regional productivity?”*. To answer this question, I used an experimental approach in which I independently manipulated dispersal and a stressor flux in two-patch metaecosystems of micro-algae.

In chapters 3 and 4, I investigated the effect of stress and dispersal on local and regional diversity and productivity in two-patch metacommunities, where dispersal was manipulated by applying different dispersal rates among patches. However, communities are typically embedded in spatially-connected landscapes. Many of those landscapes are subject to decreasing connectivity through habitat destruction and increasing fragmentation. Studies are thus needed that manipulate the number of connections among communities. Some studies have recently addressed how connectivity affects diversity in spatially-extended landscapes, mainly using homogeneous (Seymour et al. 2015) or heterogeneous landscapes where patch sizes or disturbance intensity was manipulated (Carrara et al. 2012, 2014). However, studies in which heterogeneity is manipulated by agents that show species-specific effects, such as chemical stressors, are lacking. Moreover, previous studies only applied 2 connectivity levels, which might be too low to find high-order, such as hump-shaped relationships among dispersal and diversity or dispersal and productivity. In **chapter 5**, I therefore address the question: *“How does connectivity affect the diversity and productivity in spatially connected landscapes exposed to chemical stress?”*. To deal with this question, I manipulated stressor exposure and connectivity in complex landscapes with communities of micro-algae and determined the effect of connectivity on local and regional diversity during the experiment.

In **chapter 6**, I summarize the main results of this dissertation. Furthermore, I describe the main contribution of my studies in ecological research, and I formulate some recommendations for future work. Last, I also discuss how this dissertation may have consequences for the ecological risk assessment of chemicals.

2

Non-additive effects of dispersal and selective stress on structure, evenness and biovolume production in marine diatom communities.

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Abstract

Changes in environmental conditions can impose stress that alters the structure and function of communities. However, ecologists are only starting to explore how stress can interact with dispersal. In this study, we tested how dispersal affects the structure, diversity (evenness) and function (productivity) of marine diatom communities (*Bacillariophyceae*) exposed to herbicide stress using a mainland-island framework. In a microcosm experiment, we manipulated the sequence (5 levels) and speed (two dispersal levels) of species arrival under no-stress conditions and two levels of stress. When stress was absent or low, priority effects regulated community dynamics, keeping the densities of new arrivals low. Consequently, evenness was lower in dispersed than non-dispersed communities. Moreover, because of strong local interactions, dispersal decreased productivity under no-stress conditions and low stress. Under high stress, the selection for tolerant species regulated community dynamics. This generated a decrease in evenness but buffered productivity by compensating for the loss of sensitive species. Our results show that (1) dispersal reduced evenness, but that the underlying mechanisms depend on the stress-level, (2) dispersal can function as a spatial insurance against local changes in environmental conditions. Accounting for regional processes is therefore essential for estimating the consequences of environmental changes for ecosystem functions.

2.1 Introduction

Anthropogenic factors of environmental change such as eutrophication, chemical pollution, or climate warming are major drivers of community dynamics (Vörösmarty et al. 2010, Malaj et al. 2014, Pimm et al. 2014). The way environmental change affects community structure depends on local processes, i.e. the response of the locally occurring species and their interactions (Ives 1995, Naeem and Li 1997). Environmental change alters community structure by affecting species differently. These changes in fitness lead to a species turnover and shifts in relative abundances, which can result in altered evenness and local extinctions of stress sensitive species (Hillebrand et al. 2008, Viaene et al. 2013, Mensens et al. 2015). How species turnover affects productivity depends on the capacity of tolerant species to compensate for the functional loss of sensitive species (May 1974, Flöder et al. 2010). The probability for such functional compensation increases with initial richness because of the higher probability that a stress tolerant species is present (Naeem and Li 1997, Yachi and Loreau 1999, Steudel et al. 2012).

Not only local, but also regional processes such as dispersal and colonization can alter community dynamics. If dispersal rates are very low, dispersal limitation hinders the introduction of new species into a local site. As a result, most species remain absent from that site (Cornell and Lawton 1992, Tilman 1994). When the dispersal rate increases, new species can be introduced into a local site, but their colonization success depends on local conditions (Drake 1991, Law and Morton 1996). Hence, dispersal can add a species to a local community only if dispersal rates exceed that species' local extinction probability (Shurin 2000).

There is mounting evidence that the influence of regional processes on community dynamics can depend on the order and timing of past events, termed historical contingency (Chase 2003, Fukami and Morin 2003, Fukami et al. 2010, Fukami 2015). In that case, the effect of dispersal depends on the order and timing of species introductions. A different order of introduction can lead to different interactions between species and can thus cause large differences in community structure (Chase 2003, Fukami 2015). When early-arriving species prevent the colonization of later arriving colonizers, these differences are called priority effects (Shulman et al. 1983, Chase 2003, Fukami 2015). Those priority effects are the result of a rapid monopolization of resources, leading to high interspecific interactions. Increasing dispersal rates reduce the time for resident species to monopolize those resources, and they therefore reduce priority effects (Fukami 2015).

Effects of regional processes on community dynamics can lead to both increases and decreases of local evenness. First, dispersal can promote evenness when dispersal introduces species that are locally less abundant (Hillebrand et al. 2008). Second, dispersal

reduces evenness when a strong dominant competitor is introduced. Such a negative effect of dispersal on evenness is found in most micro-algae microcosm experiments (Matthiessen et al. 2010a, Eggers et al. 2012). Dispersal can also affect productivity. When dispersal increases local richness by the introduction of new species, dispersal leads to changing complementary and selection effects on productivity (Loreau and Hector 2001, Fox 2005). These effects often result in positive richness-productivity relationships (Cardinale et al. 2012, 2013b), but can also affect productivity negatively (Loreau and Hector 2001).

When combined, theory indicated that stress and dispersal can have non-additive effects on community structure. When dispersal introduces stress resistant species into a local community, local species that are maladapted to stressful conditions can be replaced by newly introduced species that are stress resistant (Loreau et al. 2003a). Moreover, community structure is also affected when stress reduces the strength of priority effects, through a decrease in the rate of local community dynamics (Chase 2007, Fukami 2015). Effects on community structure should often lead to non-additive effects of stress and dispersal on evenness as well, but this has not yet been empirically observed. Finally, stress and dispersal can have non-additive effects on productivity. Theory suggests that dispersal can assure spatial insurance against locally changing environments (Loreau et al. 2003a). Such spatial insurance effects have been demonstrated in several experiments (Thompson and Shurin 2012, de Boer et al. 2014).

Until now, several experiments have investigated interactive effects of stress and dispersal on diversity and productivity (Thompson and Shurin 2012, Eggers et al. 2012, de Boer et al. 2014). However, existing experimental set-ups did not allow to distinguish between resident and colonizing species. Moreover, most studies that investigated interactive effects of stress and dispersal used a metacommunity approach in which the abundances of the incoming species are the result of regional processes (e.g. Eggers et al., 2012; de Boer et al., 2014). Such experimental set-ups are realistic but hamper the evaluation of the role of priority effects in dispersal-stress interactions. Studies that simultaneously investigate priority effects, diversity and productivity are thus required (Zhang and Zhang 2007, Fukami 2015). Here, we present experimental data showing how dispersal and stress affect community structure, diversity (evenness) and productivity during the assembly process. To this end, we exposed five marine diatom communities (*Bacillariophyceae*) to the herbicide atrazine. We manipulated the timing of species introductions at 3 different dispersal regimes using a mainland-island framework. This experimental set-up enabled precise control of the dispersal rates because species could be added at equal abundances and at the same rate, irrespective of their identity. We first tested the species' sensitivities to the stressor. Then, we hypothesized that priority effects would decrease with increasing stress and dispersal levels (hypothesis 1). We

tested this hypothesis by investigating the effect of day of introduction (DoI) on the species' relative abundances, and by analyzing the effects of stress and dispersal on the contribution of the initial species to final structure. Next, we hypothesized that dispersal would reduce evenness in no-stress communities because of the supply of a dominant competitor. Similarly, we predicted a decrease of evenness in high-stress communities because of the introduction of stress tolerant species (hypothesis 2). Finally, we also predicted that dispersal would positively affect productivity in all treatments, but that dispersal effects would be considerably stronger in communities under high stress (hypothesis 3).

2.2 Materials and methods

2.2.1 *Algae strains*

Naturally co-occurring marine diatoms (*Bacillariophyceae*) were sampled in the Belgian part of the Southern Bight of the North Sea in March and September 2013 using a phytoplankton net (10 μm mesh size). All viable cells from these samples were isolated according to the protocol of Andersen (2005) and grown in f/2 medium (Guillard and Ryther 1962) composed of artificial seawater (Instant Ocean®, Aquarium Systems) supplemented with silica (30 mg L^{-1} $\text{Na}_2\text{SiO}_3 \cdot 9\text{H}_2\text{O}$). Taxa were identified to the genus level under a light microscope and cell volumes were calculated according to Hillebrand et al. (1999). Cultures were kept in a climate room ($20 \pm 1^\circ\text{C}$) with a 16h photoperiod at $35 \pm 5 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ light intensity (Lumilux® Coolwhite, Osram). New cultures were inoculated every week to keep the cultures in the exponential or early stationary growth phase.

2.2.2 *Microcosm experiment*

12 species were randomly selected from the isolated strains (Appendix A1 Table A1.1). To distinguish treatment effects from identity effects, 5 different initial communities consisting of four from the twelve selected taxa were randomly composed (Tilman 1999) (Appendix A1 Table A1.2). In addition to the no-stress no-dispersal (control) treatment, we exposed the communities to two levels of both environmental stress and dispersal for 4 weeks in a full-factorial design. Atrazine, a photosystem II inhibitor, was used as an environmental stressor, and two levels (25 and 250 $\mu\text{g L}^{-1}$) were selected based on preliminary tests to represent low and high stress. The two dispersal levels (low and high) correspond to one and two dispersal events per week. At each dispersal event, a fixed biovolume of 4 randomly chosen species was introduced into the community from atrazine-free stock cultures. There was no restriction on species identities, so species could disperse several times to the same community. For each community a different immigration order was randomly selected. Each treatment was replicated 3 times, resulting in a total of 135 microcosms (Appendix A1 Table A1.2-1.4).

100 mL Erlenmeyer flasks were used as microcosms and filled with 35 mL f/2 medium containing the appropriate atrazine concentration (Sigma Aldrich). An initial biovolume of $4 \times 10^8 \mu\text{m}^3$, evenly distributed over the 4 initial species, was inoculated in each flask. Flasks were placed in a climate room ($20 \pm 1^\circ\text{C}$) at a 16h ($35 \pm 5 \mu\text{mol photons m}^{-2}\text{s}^{-1}$) photoperiod. Erlenmeyer flasks were repositioned every few days to eliminate potential differential light effects in the climate room. At each dispersal event, $4 \times 10^8 \mu\text{m}^3$ biovolume, evenly distributed over the 4 species, was added. Measurements of phosphate, nitrate and silicate concentrations have been taken weekly (Appendix A1 Table A1.5) and showed that nutrient concentrations decreased rapidly. To avoid nutrient depletion, 60% of the growth medium was therefore replaced weekly. Moreover, medium replacement prevented stress-reduction through atrazine photolysis. Replacement of medium was performed after centrifuging 80% of medium in glass tubes at 800 rpm (acceleration 5 m s^{-2} , deceleration 3 m s^{-2}) to settle the cells (centrifuging at these settings had no detectable effect on cell viability or growth). Twice a week, 1 ml samples for biomass calculation were taken, fixed with formaldehyde (6% final concentration) and stored in 24 well plates (VWR) at 4°C until analysis. Cell densities were weekly counted using an inverse microscope and Whipple grid and biovolumes were calculated from the average cell volume (Appendix A1 Table A1.1).

2.2.3 Data analysis

Biovolume was weekly determined by cell counts as described above. Since abundances of rare species were difficult to determine accurately because of the small sample sizes, the Simpson's evenness index $E_{1/D}$ was used (Eq. 2.1) as it is less sensitive for species with low abundances (compared to the Shannon-Wiener index; Hill et al. 2003). It is noted that the latter has been used in a majority of earlier biodiversity experiments (e.g. Eggers et al. 2012, Guelzow et al. 2014).

$$E_{1/D} = \frac{1}{S \times \sum_{i=1}^n p_i^2} \quad \text{Eq. 2.1}$$

With S the richness and p_i the relative abundance of species i .

Statistical analyses were performed using mixed effect models with all models including the initial composition as a random intercept. First, statistical analyses on the species' relative abundances were considered separately for the no-dispersal and dispersal treatments. This procedure was followed because the day of introduction (DoI) of the species is a significant predictor in the dispersal treatments, while it has no meaning in the no-dispersal treatments. We used mixed effect models to determine the effect of stress on the relative and absolute abundance of all species for the no-dispersal treatments. Relative abundances are limited to the $[0,1]$ interval and we therefore used a binomial model with a logit link function. We also

added a random intercept to incorporate the effect of initial composition. Calculations were done using the MASS package in R (Venables and Ripley 2002). Absolute abundances followed a normal distribution and we therefore used a linear mixed effects model with initial composition as a random intercept. Moreover, an appropriate variance structure was added to correct for heteroscedasticity. Calculations were done using the nlme package (Pinheiro et al. 2014). The effect of stress, dispersal and DoI on the relative abundance of 7 species for the low- and high-dispersal treatments was determined using a mixed effects model using a binomial distribution with a logit link function and a random intercept for each initial composition. These calculations were done using the MASS package in R (Venables and Ripley 2002). For the analysis, we only considered seven species, since they produced over 95% of total biomass together, while the contribution of the other species was marginal. To study the effects of time, stress, and dispersal on evenness, a binomial model with a temporal correlation structure was applied, using the geepack package in R (Yan 2002, Yan and Fine 2004, Højsgaard et al. 2006). Biovolume was log transformed and effects of time, stress and dispersal on log biovolume were analyzed using a linear mixed effects model with a temporal correlation structure and an appropriate variance structure to correct for heteroscedasticity using the nlme package in R (Pinheiro et al. 2014).

For the regression models of evenness, biovolume and the absolute species abundances, backward model selection was applied, based on Akaike's Information Criterion using the protocol of Zuur et al. (2009). The normality and homoscedasticity assumptions for model residuals were tested by a QQ-plot and by plotting the residuals against each predictor. The glmmPQL function in the MASS package does not allow the calculation of the Akaike's Information Criterion because the MASS package does not use a likelihood estimation for parameter estimations. Instead, it used a penalized quasi-likelihood estimation based on Laplace's approximation and Taylor series expansions. Hence, we selected the appropriate model by deleting the non-significant terms (10% confidence interval). Afterwards, we checked the model fit by plotting the residuals and experimental data against each predictor. All models and model validation figures are presented in Appendix A2.

2.3 Results

2.3.1 *Species tolerance to stress*

Species were differently affected by stress (Fig. 2.1, Appendix A1 Table A1.6-A1.7). Those differences were caused by both direct responses to the toxicant and indirect responses by altered species interactions. A majority of the species was negatively affected by stress and had lower biovolumes and lower relative abundances. However, the effect on the absolute abundances was strongest for species 2, 4 and 5, which were most sensitive (Appendix A1

Table A1.7). In contrast, some species were positively affected by stress (species 7 and 8) and obtained higher biovolumes and relative abundances in stress than no-stress treatments. Other species were barely affected by the toxicant. Because the initial communities were composed differently, each community was affected differently by the stressor. This resulted in small shifts in community structure for 2 initial species compositions (A and C) and strong shifts in community structure for the 3 other initial species compositions (B, D and E).

2.3.2 Effect of the day of introduction on the species' relative abundances

The effect of the day of introduction (DoI) on the relative species abundances in open communities was only considered for the seven species that together produced at least 95% of total biovolume, while the contribution of the other species was marginal (about 1% per species). The square root of the day of introduction (DoI) was a significant predictor of the abundance of all species, with a later introduction (higher square root-transformed DoI) leading to a lower relative abundance, thus suggesting a priority effect (Fig. 2.2, Table 2.1, Appendix A1 Table A1.8). For five out of the seven species, there was a positive interactive effect between high stress and DoI, confirming hypothesis 1 and thus suggesting a weaker priority effect at higher stress. For 2 species, there was a positive interactive effect between high dispersal and DoI, suggesting a weaker priority effect at higher dispersal.

2.3.3 Contribution of initial species to final community structure

Stress and dispersal negatively affected the contribution of initial species to final community structure (Fig. 2.3a, Table 2.2). This again indicates weakening of priority effects with increasing stress and dispersal levels (hypothesis 1). However, there was an interactive effect between stress and dispersal. This resulted in a slightly positive effect of low stress on the contribution of initial species at high dispersal. Moreover, the negative effect of high stress was stronger at low than at high dispersal.

2.3.4 Evenness

Dispersal reduced evenness, regardless of the stress level (hypothesis 2) (Fig. 2.3b, Table 2.3). This reduction was generally slightly stronger in the no-stress than stress communities. In communities without dispersal, we did not find any effect of stress on evenness.

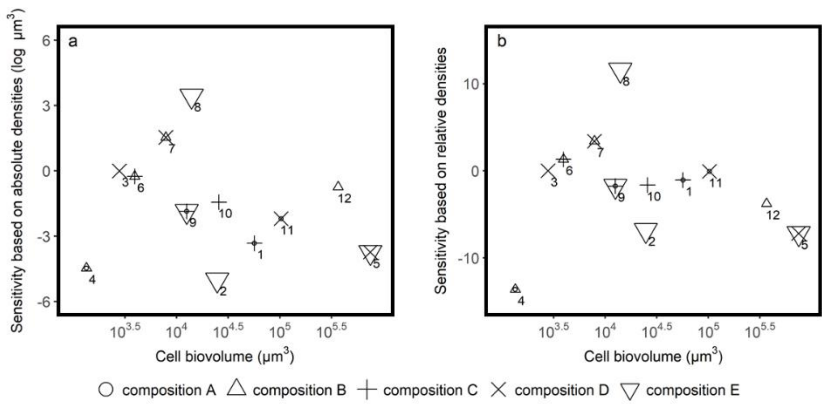


Fig. 2.1. Sensitivity of the 12 species as function of their cell biovolume. Sensitivity was calculated using a regression model of (a) the effect of high stress on the species' absolute densities in the no-dispersal treatments (log scale); (b) the effect of high stress on the species' relative densities in the no-dispersal treatments (logit scale). For the results of the statistical analyses, see Appendix A1 Table A1.6-S1.7. The number next to each symbol represents the respective species (Appendix A1 Table A1.1) and each species is depicted in the figure as many times as it appears in a community. Communities are represented by symbols.

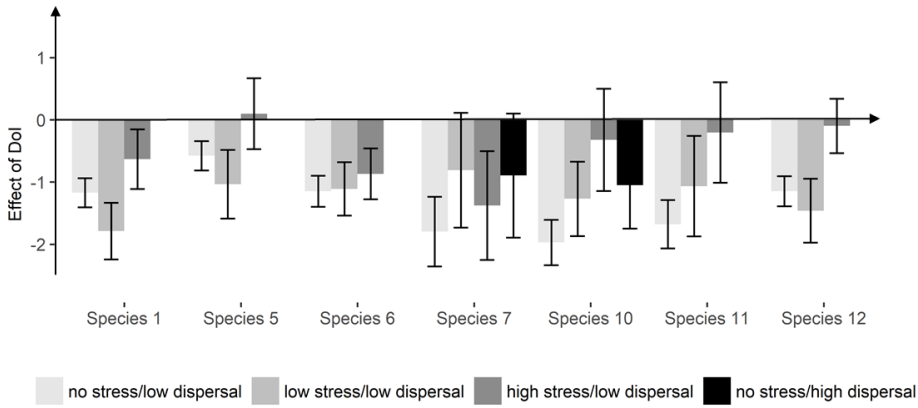


Fig. 2.2. Effect of the square root of stress, dispersal, Day of Introduction (DoI) and the interactions on the relative densities of seven species in the dispersal treatments. A stronger effect of DoI indicates stronger priority effects. Results are only shown when significant.

Table 2.1. Results of the linear models of relative species abundances using a binomial model with logit link function. The number and symbol represent the slope of the corresponding factor and the significance level respectively. Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, † $p < 0.10$. ‘Dol’: Day of introduction. ‘-’: Statistical test did not include this factor into the analysis.

factor	Species 1	Species 5	Species 6	Species 7	Species 10	Species 11	Species 12
Low stress	0.212	1.662 ***	0.220	-1.620***	-2.61***	0.003	1.594*
High stress	-2.934***	-1.743*	0.335	1.873***	-6.67***	-2.676***	-0.997†
High dispersal	-0.542**	-0.658†	0.473	-2.271***	-1.15**	-0.616**	0.394
Dol	-1.172***	-0.577*	-1.148***	-1.797***	-1.97***	-1.677***	-1.146***
Low stress x Dol	0.614**	-0.457	0.037	0.987**	0.70**	0.612	-0.314
High stress x Dol	0.540*	0.676*	0.280†	0.421	0.37***	1.473***	1.048***
High dispersal x Dol	-	-	-	0.902 *	1.65***	-	-
Low stress x high dispersal	-	-	-0.222	1.645*	-	-	-1.231†
High stress x high dispersal x Dol	-	-	0.830*	1.933***	-	-	-1.339*
Low stress x high dispersal	-	-	-	-1.653	-	-	-
Low stress x high dispersal x Dol	-	-	-	-0.805†	-	-	-

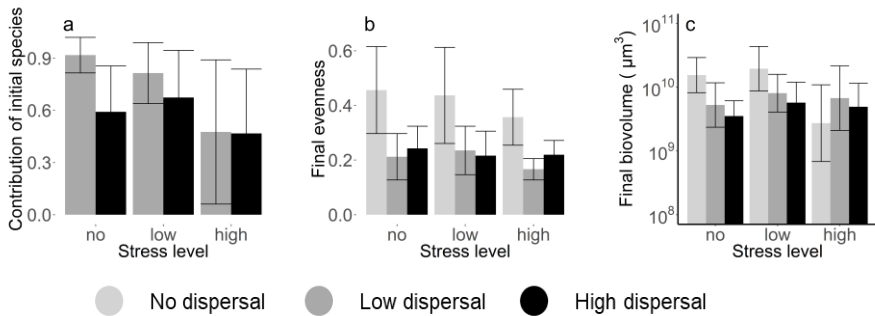


Fig. 2.3. (a) Contribution of initial species, (b) final evenness and (c) final biovolume as function of stress level for 3 dispersal levels on day 28. A high contribution of initial species indicates strong priority effects.

Table 2.2. Result of the linear model of the contribution of initial species to final biovolume on day 28 using a binomial model with logit link function.

factor	mean	sd.	p-value
Intercept	2.913	0.770	<0.001
Low stress	-0.935	0.519	0.076
High stress	-2.988	0.506	<0.001
High dispersal	-2.456	0.506	<0.001
Low stress x high dispersal	1.434	0.646	0.029
High stress x high dispersal	2.405	0.625	<0.001

Table 2.3. Results of the linear models of evenness using a binomial function, and of the logarithm of biovolume using a generalized linear model. Time 0 corresponds to day 7 (first day of measurement). '-': this factor was not included into the analysis based on the Wald-test.

factor	Evenness			Log biovolume		
	Value	Sd.	p-value	Value	Sd.	p-value
Intercept	1.252	0.168	<0.001	9.551	0.063	<0.001
Time	-0.060	0.008	<0.001	0.063	0.009	<0.001
Time^2	-	-	-	-0.002	0.000	<0.001
Low stress	0.117	0.143	0.417	0.131	0.109	0.227
High stress	-0.278	0.206	0.176	-0.890	0.129	<0.001
Low dispersal	-0.997	0.139	<0.001	0.047	0.078	0.544
High dispersal	-1.021	0.128	<0.001	0.138	0.075	0.067
Time x low stress	-	-	-	-0.015	0.015	0.347
Time x high stress	-	-	-	-0.048	0.018	0.007
Time^2 x low stress	-	-	-	0.001	0.001	0.292
Time^2 x high stress	-	-	-	0.002	0.001	0.003
Time x low dispersal	-	-	-	-0.023	0.006	<0.001
Time x high dispersal	-	-	-	-0.037	0.006	<0.001
Low stress x low dispersal	0.181	0.095	0.056	0.053	0.135	0.694
High stress x low dispersal	0.440	0.163	0.007	-0.020	0.159	0.900
Low stress x high dispersal	-0.018	0.149	0.904	-0.186	0.130	0.153
High stress x high dispersal	0.398	0.225	0.077	-0.280	0.153	0.070
Time x Low stress x low dispersal	-	-	-	0.006	0.010	0.590
Time x Low stress x high dispersal	-	-	-	0.012	0.010	0.220
Time x high stress x low dispersal	-	-	-	0.051	0.012	<0.001
Time x high stress x high dispersal	-	-	-	0.042	0.012	<0.001

2.3.5 Biovolume

Except for day 7, dispersal reduced productivity in the no-stress treatments but affected productivity positively in the high-stress treatments (Fig. 2.3c, Table 2.3). The negative effect of dispersal on productivity after day 7 is the result of a productivity decrease for low and high dispersal. In contrast, biovolume increased during the whole experiment in the no-dispersal treatments. Stress had a negative effect on biovolume (Fig 2.3c, Table 2.3). However, we found significant interactions between time, stress, and dispersal, suggesting that stress and dispersal had a non-additive positive effect on biovolume that became stronger with time.

2.4 Discussion

2.4.1 The combined effects of stress and dispersal on community structure

The effect of day of introduction on the species relative abundances and the high contribution of initial species indicate strong priority effects in the low-dispersal no-stress communities. However, the effects of both predictors became weaker at high stress and high dispersal, which indicates a decrease of priority effects with stress and dispersal (hypothesis 1).

Coexistence theory states that competition for a common resource can lead to the competitive exclusion of all but the most dominant species (Tilman 1982, Chesson 2000). In our experiment, all species are marine diatoms, using the same macro-nutrients (Bruno et al. 2006, Schmidtko et al. 2010, Mensens et al. 2015). Therefore, one would expect to find dominance of the best competitive species and thus low priority effects across all factor combinations. However, a high similarity in traits among species can benefit priority effects. For example, Zhang & Zhang (2007) demonstrated that relatively small differences in monoculture yield can lead to long-lasting priority effects in two-species algae communities. Nevertheless, slight differences in competitive strength are expected to ultimately result in the dominance of the strongest competitor, erasing priority effects. Even so, in the case of only small differences in competitive strength, transient phenomena can be very long-lasting (Hastings 2004) and are thus also important for understanding historical contingency in community assembly (Fukami and Nakajima 2011).

The negative effect of high dispersal on priority effects corroborates the theoretical finding that, when dispersal rates increase, communities exhibit weaker priority effects (Fukami 2015). Similar results were found in both plant and zooplankton communities in which longer delays between subsequent species arrivals resulted in stronger priority effects (Körner et al. 2008, Symons and Arnott 2014).

The lower priority effects we found at high stress are due to various reasons (Chase 2003, 2007). First, species that are very sensitive to the stressor are not able to persist (e.g. species 4, 5 and 8; Fig. 2.1). Because fewer species can persist, there are fewer possible community compositions (Chase 2007). Second, stress decreases growth rates. It thus takes longer for the early-introduced species to achieve high densities (Table 2.3). Therefore, early-introduced species only use a small amount of the resources, which are consequently available for later arriving species (Gross et al. 2005, Symons and Arnott 2014). Third, species that are tolerant to stress are often poorer competitors because of trade-offs (Tilman 1994). Therefore, they are less likely to hinder establishment of other species through interspecific interactions. Unfortunately, we cannot verify this in our experimental system, as we did not measure competitive strength among species.

Surprisingly, low stress had a small positive effect on the abundance of initial species at high dispersal. This can be due to a higher productivity on day 4 (day of first dispersal event at high dispersal) in the low- than in the no-stress community. Such a slightly higher productivity could have decreased the colonization opportunity for species that arrived on day 4. This phenomenon, in which stress generates a higher productivity at low than no stress, is termed the hormesis effect (Kaiser 2003) and has been observed before in algae communities exposed to chemical stressors (Pomati and Nizzetto 2013). Finally, the abundance of the initial species to final biovolume was not affected by dispersal at high stress. This was probably due to the very weak priority effects at high stress.

2.4.2 The combined effects of stress and dispersal on evenness

As was predicted, dispersal affected evenness negatively (hypothesis 2). Negative effects of dispersal on evenness are commonly caused by the regional distribution of a dominant species (Matthiessen et al. 2010a, Eggers et al. 2012). However, in our experiment, such a negative effect was caused by the strong priority effects in the no- and low-stress communities. Those priority effects generated large differences in abundance between initially present species and later arriving species. Such a discrepancy in abundance caused the low evenness we observed.

As priority effects were low in high-stress communities, they cannot explain the negative effect of dispersal on evenness in those communities. Instead, dispersal reduced evenness in high-stress communities because of the introduction of stress-tolerant species that dominated the communities at the expense of the stress-sensitive species. Similar results were found by Eggers et al. (2012) in communities affected by a heat wave. Thompson & Shurin (2012) found no effects of dispersal on diversity in communities under salt stress, and positive dispersal effects in communities under heat stress. However, this positive effect was largely caused by

an increase in richness, while a separate analysis on how dispersal affects evenness was not presented. This demonstrates the need for studies that examine stress and/or dispersal effects on evenness (Hillebrand et al. 2008).

The absence of a stressor effect on evenness at no dispersal was unexpected, because stress strongly affected community structure. In order to understand this result, it should be noted that stress can have both positive and negative effects on evenness, where the sign of this effect is community-dependent. Stress affects evenness negatively when it increases fitness differences because of a high difference in stress tolerance (e.g. community D and E, Appendix A1 Fig. A1.2, see also e.g. Viaene et al. 2013). In contrast, stress affects evenness positively when it equalizes fitness differences by suppressing the dominant species (e.g. community B, Appendix A1 Fig. A1.2, see also e.g. Knauert et al. 2009). In our experiments, we observed both types of effect (positive and negative), so that the average effect of stress on evenness in the no-dispersal treatments did not significantly differ from zero.

2.4.3 The combined effects of stress and dispersal on productivity

Hypothesis 3 postulated a positive effect of dispersal on productivity. Based on our results, we could not accept this hypothesis. Even though dispersal positively affected productivity at high stress, dispersal effects on productivity switched from positive (week 1) to negative (week 2 to 4) at low and no stress. The initial positive effect, which is due to an earlier peaking of biovolume in open communities, could be explained by a rapid growth after introduction on day 4 because of low competition and abundant resources. The subsequent lower productivity in open compared to closed communities contradicts our hypothesis that dispersal would affect productivity positively. However, dispersal rates in most of the previous studies that examined dispersal-productivity relationships depended on regional dynamics (e.g. Matthiessen & Hillebrand, 2006; Matthiessen et al., 2010), while in our design dispersal rates were manipulated directly, ensuring equal dispersal abilities among species. Therefore, the lower biovolume in open treatments observed in our study was probably induced by strong local competitive dynamics. As dispersal increased local richness and productivity in the first week, interspecific competition may have increased, consequently reducing productivity. This negative relation between richness and functioning is commonly found in phytoplankton communities because of a strong niche overlap and strong interspecific interactions (Bruno et al. 2006, Schmidtke et al. 2010, Mensens et al. 2015).

Even though dispersal and high stress decreased productivity, the combination of both attenuated these negative effects. This suggests that combined dispersal and stress is non-additive, i.e. dispersal buffers productivity against toxicity. Such buffering effect can be a consequence of functional compensation (Tilman et al. 1997) in which stress-tolerant species

compensate for the loss of sensitive species. A higher dispersal rate – and thus a higher local richness – increased the probability that stress-tolerant species were present, which facilitated functional compensation. For example, in composition A, none of the initial species was stress tolerant, leading to a low biovolume at no dispersal (Appendix A1 Fig. A1.1). When stress tolerant species 6 and 12 entered the community, biovolume increased (Appendix A1 Fig. A1.1-A1.2). Dispersal thus created spatial insurance by increasing diversity (Loreau et al. 2003a), as was already demonstrated in studies with algae (de Boer et al. 2014) and zooplankton (Thompson and Shurin 2012, Symons and Arnott 2013) communities.

In our study, functional compensation was also observed in closed communities under stress. Here, productivity was relatively well preserved in communities where the most dominant species was stress tolerant (e.g. composition C, where biovolume at high stress was 20% of the control; Fig. 2.1, Appendix A1 Fig. A2.1-A2.2), or the loss in functioning of the sensitive dominant species was compensated by a tolerant species (e.g. composition B, where biovolume at high stress was 69% of the control; Fig. 2.1; Appendix A1 Fig. A1.1-A1.2). Such a compensation by the resident species limits the compensatory role of dispersal.

2.4.4 Conclusion and outlook

In this study, we demonstrated that stress affected the community assembly process by simultaneously weakening priority effects and strengthening selection. This resulted in strong negative effects of dispersal on evenness and non-additive effects between stress and dispersal on productivity. Strong priority effects were due to large niche overlap in our study system. Further studies are therefore needed to investigate if selection factors can mediate priority effects during community assembly in communities governed by weaker (e.g. grasslands, Hector et al., 1999; De Boeck et al., 2008) or even positive interactions (e.g. facilitation, Brooker et al., 2008).

We showed that dispersal can maintain productivity in stressed conditions because of the introduction of stress tolerant species. However, our results indicate that the consequent shifts in community structure can also have negative effects on the dynamics following release from stress, which we did not test here. Indeed, when stressor concentrations decrease, stress tolerant species can hinder the introduction of the species that were present before the stress event because of the same priority effects we observed here. Such mechanisms could have a major impact for restoration decisions.

Many communities today suffer exposure to and effects from environmental stressors, including organic chemicals (Beketov et al. 2013, Malaj et al. 2014). Our results show that the effects of dispersal, and the potential interactions with selective stress, need to be accounted

for to allow a better understanding of how biodiversity and ecosystem functioning respond to stress.

3

The effect of stress heterogeneity on the relationship between dispersal and diversity

Abstract

Many theoretical models predict a hump-shaped relationship between dispersal and local diversity in heterogeneous environments. However, the effects of the underlying factors (the degree of environmental heterogeneity, the interspecific variation in stress response, and heterogeneous starting compositions among patches) on this relationship is less well understood. We used a game-theoretic metacommunity model to simulate the relationship between dispersal and diversity for 200 metacommunities to investigate the proportion of hump-shaped relationships between dispersal and diversity across various factor combinations: stress heterogeneity, interspecific variation in stress response and heterogeneity of the starting composition. The proportion of hump-shaped relationships was highest at an intermediate stress heterogeneity for the low-stressed community, but increased with an increasing stress heterogeneity for the high-stressed community. The effect of stress heterogeneity on the proportion of hump-shaped relationships increased when the interspecific variation of the stress response increased. Moreover, when the starting composition was heterogeneous, hump-shaped relationships also appeared at a low stress heterogeneity. These results suggest that the prevalence of the often-assumed hump-shaped relationship between dispersal and diversity strongly depends on how environmental and biological spatial heterogeneity interact with local community dynamics under stress.

3.1 Introduction

The composition and diversity of communities is regulated by both local and regional processes (Robert and Wilson 1967, Levin 1992, Leibold et al. 2004). How those processes interact is investigated using the metacommunity framework (Leibold et al. 2004, Holyoak et al. 2005). This framework proposes dispersal to show a hump-shaped relationship with diversity in heterogeneous landscapes through mass effects (Mouquet and Loreau 2002, 2003, Loreau et al. 2003a, Mouquet et al. 2006). When dispersal is absent, environmental heterogeneity creates spatial differences in community composition, generating a low local diversity as competitive superiors dominate their preferred local community. Increases in dispersal generate a higher local diversity as dispersal introduces immigrants, allowing the persistence of species that would otherwise have been excluded (Mouquet and Loreau 2003, Leibold et al. 2004). Large increases of dispersal cause local diversity to decrease again because dispersal homogenizes the metacommunity and the strongest regionally dominant species starts excluding regionally subdominant species. Hump-shaped relationships are expected to mainly occur at an intermediate environmental heterogeneity (Kunin 1998, Mouquet et al. 2006). When environmental heterogeneity is too low to create spatial differences in composition, no hump-shaped dispersal-diversity relationships appear. When environmental heterogeneity is too strong, species differ so strongly in competitive abilities that no regional exclusion occurs.

Differences in stress intensity among patches create environmental heterogeneity by affecting composition and population sizes. First, how stress affects the composition of communities, depends on the response of the species to stress. Species occupy different niches along an environmental gradient. Therefore, a change of the environment can expose some species to stress, decreasing the performance of those species, while it may increase the performance of others (Colwell and Fuentes 1975, Woodward et al. 2010). Moreover, species may show a variation in niche widths along an environmental gradient. Hence, a change of the environment can induce a strong stress response in some species, while it may only generate a weak response in others (Bolnick et al. 2010, De Laender et al. 2016). As the interspecific variation in stress responses affects composition, it also influences the effect of dispersal on diversity (Gilbert 2012). By reducing population sizes, stress is likely to reduce the number of organisms that emigrate from a stressed community, reducing mass effects. Moreover, when population sizes are small, these populations are more vulnerable to stochastic extinctions (Lande 1993, Schreiber and Lloyd-Smith 2009, Huang et al. 2015). Stress might hence affect the number of species that can emigrate from high-stressed communities.

When the starting composition is homogeneous, all species are initially present in all communities. As a result, species sort along the communities and competitive superiors dominate their preferred local community (Mouquet and Loreau 2002, 2003). However, when the starting composition is heterogeneous, dispersal limitation prevents species from colonizing their suitable patch (Shurin 2000). Hence, a higher dispersal rate is expected to increase local diversity by introducing species to patches where they were initially not present. High dispersal then decreases local diversity when dispersal redistributes dominant species while excluding regionally subdominant species, generating a hump-shaped relationship between dispersal and diversity (Kneitel and Miller 2011, Severin et al. 2013).

Despite the high number of theoretical studies that investigate the relationship between dispersal and diversity in heterogeneous landscapes (Mouquet and Loreau 2003, Loreau et al. 2003a, Mouquet et al. 2006, Haegeman and Loreau 2014), no studies exist that investigate how stress heterogeneity influences this relationship. In contrast to theoretical studies, empirical studies do exist that investigate the relationship between dispersal and local diversity by manipulating factors such as random disturbances, light intensity, temperature or chemical stress. These studies can be considered to create stress heterogeneity, generating differences in community composition and population sizes (e.g. Matthiessen et al. 2010a, b, Altermatt et al. 2011, Eggers et al. 2012, Limberger et al. 2014). Moreover, theoretical models do mostly not integrate how the interspecific variation in responses to environmental heterogeneity affect diversity-dispersal relationships. However, environmental niches have a strong effect on community composition, potentially affecting the relationship between dispersal and diversity (Gilbert 2012). Last, most theoretical studies start with the assumption that without dispersal each community is dominated by the strongest competitor (Mouquet and Loreau 2003, Loreau et al. 2003a, Haegeman and Loreau 2014). However, starting compositions in empirical studies are often heterogeneous among communities (Grainger and Gilbert 2016), and dispersal might affect the relationship between dispersal and diversity by adding new species in their suitable patch (Kneitel and Miller 2011).

In the present study, we investigate how stress heterogeneity, interspecific variation in stress response and starting composition affect the relationship between dispersal and local diversity. To do so, we used a stochastic model (Huang et al. 2015). We performed 200 iterations, each iteration representing a metacommunity of micro-algae. We defined environmental stress on a community level as a reduction of the average per-capita birth rates. Stress heterogeneity was applied in two-patch metacommunities containing a low-stressed and high-stressed community. We manipulated the magnitude of the stress heterogeneity, the interspecific variation of the stress response, and the starting composition (homogeneous vs heterogeneous) according to a full-factorial design. Per iteration and factor combination we

then simulated community dynamics at several dispersal rates and tested if the relationship between dispersal and diversity was positive, negative or hump-shaped. This allowed us to examine if the proportion of hump-shaped relationships depended on the considered factors. Last, we examined if the dissimilarity in composition and abundance ratio between the low-stressed and high-stressed community could explain our results.

We expected that the magnitude of stress heterogeneity would change the proportion of hump-shaped relationships between dispersal and diversity. For the high-stressed community, the proportion of hump-shaped relationships is expected to be highest at a high stress heterogeneity because of an increasing dissimilarity in community composition. For the low-stressed community, the proportion of hump-shaped relationships is expected to be highest at an intermediate stress heterogeneity. At a low stress heterogeneity, the proportion of hump-shaped relationships would increase because of an increase in dissimilarity in composition in the unstressed and stressed communities. However, at a high stress heterogeneity, the proportion of hump-shaped relationships would decrease in the low-stressed community because of a lower population size in the high-stressed than in the low-stressed community. We also expected that an increasing interspecific variation of the stress response would increase the proportion of hump-shaped relationships as species would respond more differently to a change in stress intensity. Last, we expected that a heterogeneous starting composition would increase the proportion of hump-shaped relationships.

3.2 Methods

3.2.1 Model

The model is an extension of the stochastic community model of Huang et al. (2015). In the original model, local community dynamics are assumed to be driven by birth (1), death (2) and species interactions (3, 4), resulting in 4 different processes:

$$X_{i,j} \rightarrow X_{i,j} + X_{i,j} \quad (1) \qquad X_{i,j} \rightarrow 0 \quad (2)$$

$$X_{i,j} + X_{k,j} \rightarrow X_{k,j} \quad (3) \qquad X_{i,j} + X_{k,j} \rightarrow X_{i,j} \quad (4)$$

With $X_{i,j}$, $X_{k,j}$ an individual of species i and k respectively, $i, k \in \{1, \dots, n\}$ with n the number of species, in community j with $j \in \{1, 2\}$ for a two-patch metacommunity. Processes 1 and 2 occur at the birth rate $b_{i,j} [d^{-1}]$ and the death rate $d_{i,j} [d^{-1}]$ respectively. Rates of competitive displacement in (3) and (4) occur at a rate $a_{i,k,j} [d^{-1}]$ and $a_{k,i,j} [d^{-1}]$ respectively (Huang et al. 2015).

We extended this model with two regional processes: in two-patch metacommunities, every individual can move from patch 1 to patch 2 and vice versa (5, 6).

$$X_{i,1} \rightarrow X_{i,2} \quad (5) \quad X_{i,2} \rightarrow X_{i,1} \quad (6)$$

Processes 5 and 6 occur at a rate $m_{i,1 \rightarrow 2} [d^{-1}]$ and $m_{i,2 \rightarrow 1} [d^{-1}]$ respectively. If the death rate $d_{i,j}$ and interaction rate $a_{i,k,j}$ do not depend on patch identity, and the dispersal rates $m_{i,1 \rightarrow 2}$ and $m_{i,2 \rightarrow 1}$ are independent of both patch and species identity, the transition rates can be written as:

$$T_{i,j}^{l+} = b_{i,j} N_{i,j} \quad \text{Eq. 3.1}$$

$$T_{i,j}^{l-} = d_i N_{i,j} + N_{i,j} \sum_{k=1}^n a_{i,k} N_{k,j} \quad \text{Eq. 3.2}$$

$$T_{i,1}^{r+} = T_{i,2}^{r-} = m N_{i,2} \quad \text{Eq. 3.3}$$

$$T_{i,2}^{r+} = T_{i,1}^{r-} = m N_{i,1} \quad \text{Eq. 3.4}$$

With $b_{i,j}$ the patch-dependent birth rate. $T_{i,j}^{l+}$ and $T_{i,j}^{l-}$ represent the rate at which each species i in community j respectively increases or decreases its abundance $N_{i,j}$ by one individual through local processes l . $T_{i,1}^{r+}$, $T_{i,2}^{r+}$, $T_{i,1}^{r-}$ and $T_{i,2}^{r-}$ represent the rate at which each species i in community 1 or 2 respectively increases or decreases its abundance $N_{i,j}$ by one individual through regional processes r . The Master and differential equations are given in Appendix B1. Stochastic fluctuations occur around the equilibrium population abundance in the system which can be determined using a spatially-extended Lotka-Volterra model (Altermatt et al. 2011b). Appendix B2 represents the comparison of the output of the stochastic model and the spatially-extended Lotka-Volterra model. The birth rate $b_{i,j}$ is the only parameter that depends on patch identity, as it is a function of the environmental value E in patch j . $b_{i,j}$ is a function of the environment according to:

$$b_{i,j} = b_{0,i} f_i(E_j) \quad \text{Eq. 3.5}$$

With $b_{0,i}$ the birth rate of species i in optimal conditions. f_i is the species-specific response of the birth rate along the environmental gradient and also represents the environmental niche of species i . We used a normalized gamma distribution to restrict f_i between 0 and 1 and to allow for both symmetrical and asymmetrical responses of the birth rate to the environment.

$$f_i(E) = \left(\frac{E}{\theta_i(k_i - 1)} \right)^{k_i - 1} e^{-\frac{E}{\theta_i} + (k_i - 1)} \quad \text{Eq. 3.6}$$

The gamma distribution is determined by a shape parameter k_i and scale parameter θ_i with niche mean $\mu_i = k_i \theta_i$ and variance $\sigma_i^2 = k_i \theta_i^2$, which represents the width of the niche.

We defined stress intensity at the community level. It was quantified along the environmental axis as a function of the species' environmental niches:

$$SI(E_j) = 1 - \frac{\sum_{i=1}^n f_i(E_j)}{\max_E(\sum_{i=1}^n f_i(E))} \quad \text{Eq. 3.7}$$

The stress intensity ranged from 0 (when species performed on average optimally) to 1 (severely stressed conditions when species performed on average worst). Because the environmental niches follow a gamma-distribution, the stress-intensity follows a unimodal or multimodal pattern along the environmental gradient (Fig. 3.1). As such, the stress-intensity can obtain an identical value at different positions along the environmental gradient E .

3.2.2 Design and parameterization

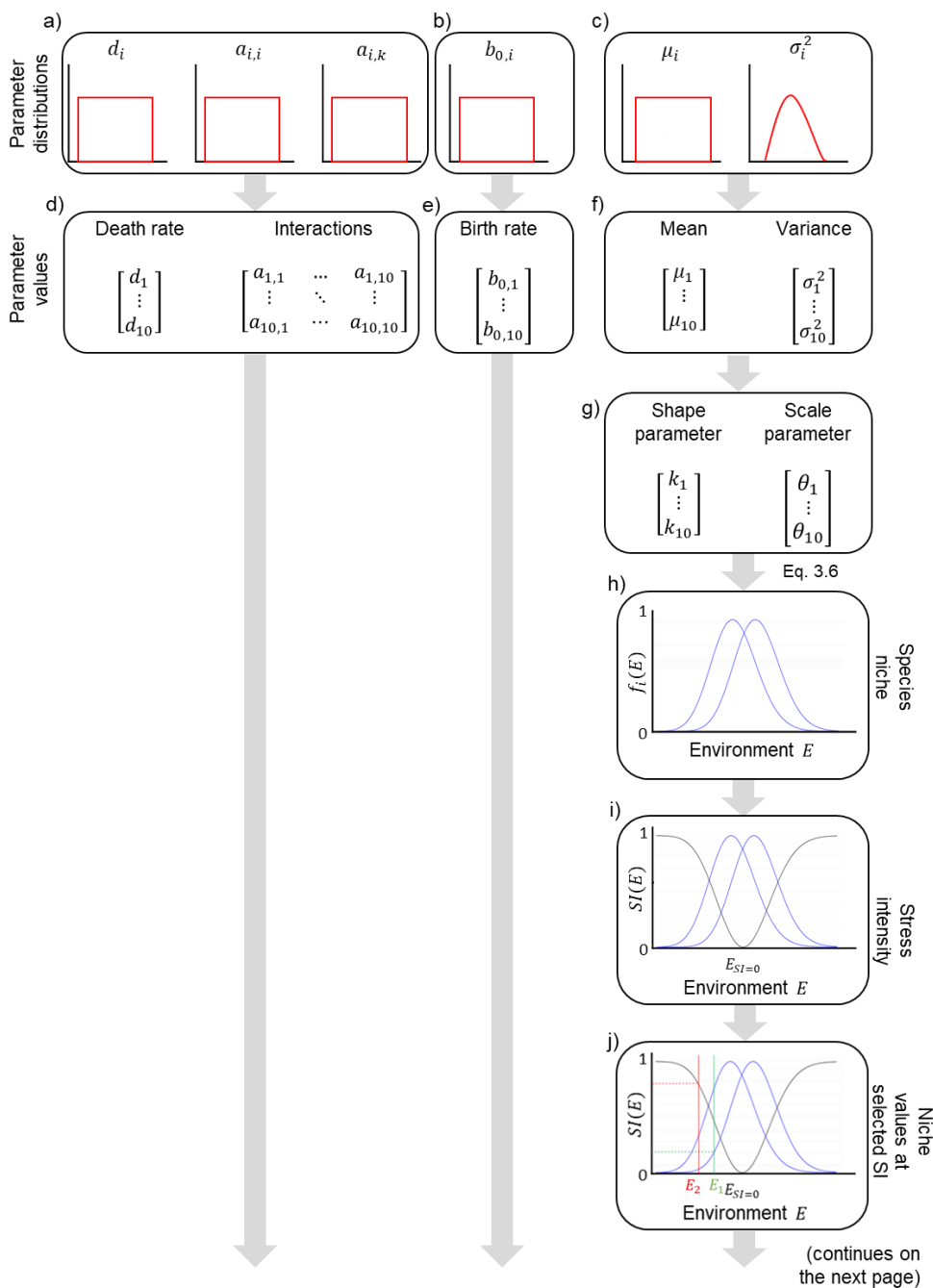
We simulated community dynamics for two-patch metacommunities. We used a full-factorial design with the following factors: dispersal rate, stress heterogeneity, the interspecific variation of the stress response (niche mean and niche width) and the initial community composition. We considered 7 levels of the dispersal rate, which varied between 10^{-6} and 10^0 in a logarithmic scale in steps of 10 and was equal for all species. We considered 6 levels of stress heterogeneity. To manipulate stress heterogeneity, stress intensity differed between two communities within the same metacommunity, while the average stress intensity was equal among metacommunities (Fig. 3.1). We created stress heterogeneity by exposing one community to a low stress intensity (low-stressed community) and one community to a high stress intensity (high-stressed community). We thus varied stress heterogeneity from low (stress intensity equal in the low- and high-stressed community) to high (stress intensity close to 0 in the low-stressed and close to 1 in the high-stressed community). The stress intensity SI was given by $\{SI_1, SI_2\} \in \{\{0.5, 0.5\}, \{0.4, 0.6\}, \dots, \{0.1, 0.9\}, \{0.05, 0.95\}\}$ with SI_1 and SI_2 the stress intensity in the low-stressed and high-stressed community respectively. Hence, the average stress intensity over the entire metacommunity was 0.5 across all levels of stress heterogeneity. E_j , the position of community j along the environmental axis depended on the stress-intensity in a community j (Fig. 3.1). Because an identical stress-intensity value could be obtained at different positions along the environmental axis, we adopted the following procedure to attain only one environmental value E_j per stress-intensity level. First, we determined $E_{SI=0}$, which is the position along the environmental axis where the stress-intensity is 0. Next, we measured the skewness of the slope of the stress-intensity curve at both sides of $E_{SI=0}$. We then selected the environmental values at the side of the curve with the highest

skewness. All environmental values were selected in a consecutive order. In other words, when skewness was highest at the left side of the stress intensity curve, a higher stress intensity resulted in a lower value of E_j . In contrast, when skewness was highest at the right side of the stress intensity curve, a higher stress intensity resulted in a higher value of E_j (Fig. 3.2). The niche mean and niche width of the environmental niche each contained three levels, each factor ranging from a low variation to a high variation. The niche mean and niche optimum were sampled from uniform and gamma distributions, respectively. The parameters of these distributions depended on the factor level that was considered. The niche mean μ_i was randomly selected from $U(95,105)$, $U(85,115)$, $U(55,145)$ for a low, average and high variation of the niche mean, respectively. The niche variance σ_i^2 was randomly sampled from the gamma distributions $G(\theta = 0.2, k = 500)$, $G(\theta = 5, k = 20)$, $G(\theta = 125, k = 0.8)$ for a low, average and high variation of the niche width, respectively. These gamma distributions have an identical mean but different variance (20, 500 and 12500 respectively). The values of the niche mean and niche variance determined the species' environmental niche and the shape of stress-intensity curve according to Eq. 3.6-3.7 (Fig. 3.1). Last, the initial community composition contained two levels. When the initial community composition was homogeneous, each community initially contained the same species. When the initial community composition was heterogeneous, local richness was initially equal, but the species composition varied so that the communities only had two species in common. The initially homogeneous and heterogeneous metacommunities had an identical regional richness.

The maximum birth rates $b_{0,i}$ and per capita mortality rates d_i were randomly sampled from $U(0,1)$ and $U(0.01, 0.1)b_{0,i}$, respectively. Similar to Baert et al. (2018), the strength of the intraspecific interactions, a_{ii} , was sampled from $U(10^{-4}, 10^{-3})$. The strength of interspecific interactions was subsequently sampled from $U(-0.01, 2)a_{ii}$.

3.2.3 Simulations

We used a Monte-Carlo simulation approach in which we performed 200 iterations per factor combination. For each iteration, we generated 10 species by randomly drawing values for $b_{0,i}$, d_i , a_{ii} , a_{ij} . The initial total abundance per community was 100 and was evenly distributed over all species in homogeneous metacommunities. We constructed the heterogeneous metacommunities by randomly drawing two species that were present in both communities. Next, we randomly selected four species for the low-stressed community and assigned the remaining four species to the high-stressed community.



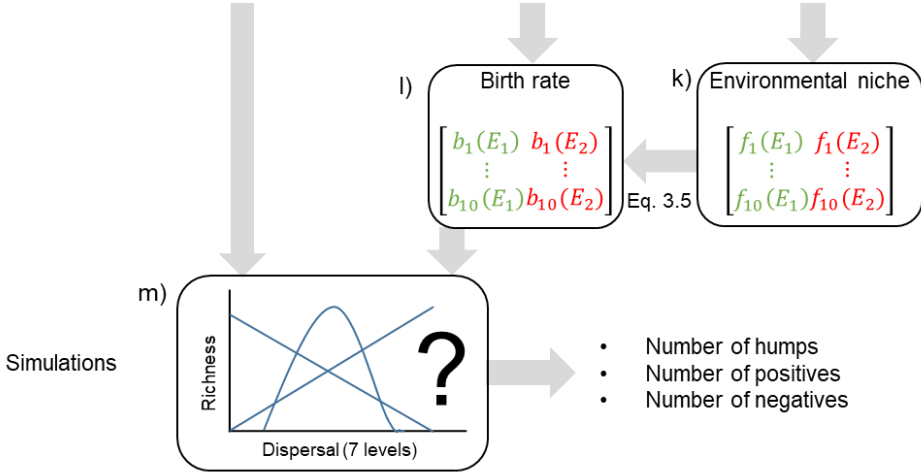


Fig. 3.1. Work flow for the design and parameterization of the model. First we randomly selected parameter values for $d_{i,j}$, $a_{i,j}$, $b_{0,i}$ and μ_i from uniform distributions and σ_i from a gamma distribution (a, b, c, d, e, f). From μ_i and σ_i , we determined the shape and scale parameter (g) to calculate the environmental niches along the environmental axis using Eq. 3.6 (h). These environmental niches are depicted in blue. Note we calculated the environmental niches for 10 species in total, while the environmental niche of only 2 species is depicted for clarity. Next, we calculated the stress intensity (black) along the environmental axis using Eq. 3.7 (i). Then we selected two stress intensities (low: green, high: red) and determined the corresponding niche values $f_i(E_1)$, $f_i(E_2)$ at the respective environmental values E_1 and E_2 (j). We obtained environmental values for the 10 species at a high (red) and a low (green) stress intensity (k). Next, optimal birth rates $b_{0,i}$ were multiplied with the environmental values $f_i(E_j)$ (l). Parameters were used to perform model simulations at 7 dispersal rates (m). Next, local richness was calculated for each community and richness values were used to fit a positive, negative or hump-shaped relationship.

Community dynamics were simulated using the Gillespie algorithm (Gillespie 1977) using the GillespieSSA package in R (Pineda-Krch 2008). We applied the tau-loup method with a fixed step size (0.02) to limit simulation times. Population dynamics reached their stationary distribution around $t = 341$. We selected this time point because it was the lowest time t_{min} for which the number of species changed on average with less than 1 species within the time interval $[t_{min}, t_{min} + 100]$. Each combination per iteration was repeated 12 times to minimize the number of factorial combinations for which no convergence of the stationary distribution could be reached. All simulations were performed using R (R. Core Team 2016).

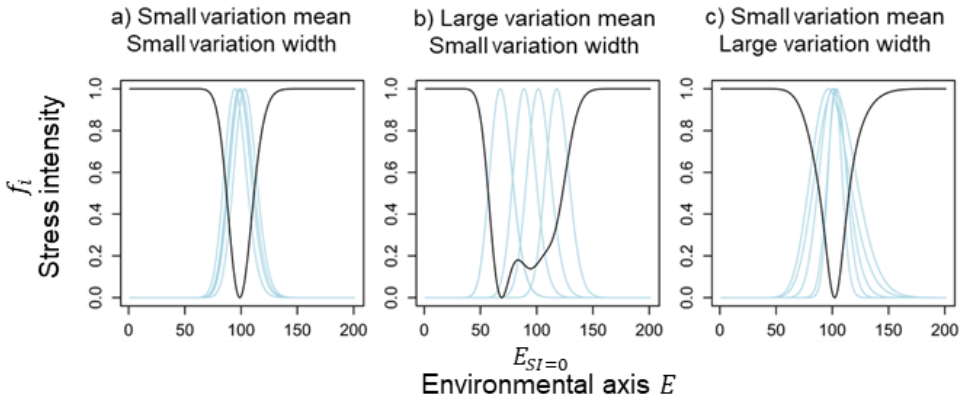


Fig. 3.2. Species environmental niche $f_i(E)$ (blue) and the stress intensity SI (black) along an environmental gradient for 5 species. In (a) all species have a similar variation of the niche mean and niche width. We applied an interspecific variation of the stress response using two approaches: In (b) we introduced the interspecific variation of the niche mean; In (c) we introduced the interspecific variation of the niche width (c). We selected the stress intensity values on the side of the stress intensity curve with the highest skewness. For instance, in panel b, we selected the stress intensity values at the right side of the environmental minimum $E_{SI=0}$, selecting the stress values at the side of the stress intensity curve with the highest skewness.

3.2.4 Analysis

For each community we measured diversity (local richness) using the vegan package in R (Oksanen et al. 2014). We then calculated the average richness of all replicates for the time interval [341, 350]. Next, we determined the relationship between dispersal and local richness for each community and measured the proportion of hump-shaped, positive and negative relationships and the proportion of relationships that did not belong to any of the previous categories (“other”) per factorial combination and for the low-stressed and high-stressed community separately. Relationships for which no convergence was achieved for at least one dispersal level were not included into the analysis (<3% of the relationships).

First, a relationship was appointed to the category “other” when the difference of the highest and lowest richness was smaller than a threshold value of 1 species. Selecting a lower threshold value increased the number of positive, negative and hump-shaped relationships, but did not change the effect of stress heterogeneity, niche mean, niche width or starting community on the proportion of hump-shaped or positive relationships (Appendix B3, Fig. B3.1, B3.2). For the remaining relationships, we determined if the relationship was monotonically increasing (i.e. positive), monotonically decreasing (i.e. negative) or if it had one maximum (i.e. hump-shaped). We defined a maximum as a value below which dispersal

monotonically increased diversity and above which dispersal monotonically decreased diversity. Next, we performed a second analysis by using the remaining relationships. We fitted a first and second-order model with richness as the response variable and the log transformed dispersal rate as predictor variable. If the regression coefficient was higher than 0.7 for the first-order model, the relationship was assigned as positive or negative. Next, when the regression coefficient of the second-order model was higher than 0.7, then the relationship was assigned as hump-shaped. A change of the regression coefficient within the interval [0.6,0.8] did not change the results. Last, all remaining relationships were assigned as “other”. The subsequent application of both analyses was necessary to distinguish the different types of relationships as the first method did not allow for small deviations from increasing, decreasing or unimodal relationships, while the second method did not allow to distinguish unimodal relationships that are not symmetrical.

Per metacommunity, we calculated the Sørensen dissimilarity index (based on presence-absence data) using the *betapart* package (Baselga et al. 2013). We also distinguished the nestedness and replacement component of the Sørensen index (Baselga and Orme 2012). The first indicates a different richness among communities, while the other indicates a species turnover. Next, we determined the ratio of the abundance of the high-stressed and low-stressed community. We plotted the proportion of hump-shaped relationships as function of the dissimilarity index and log transformed abundance ratio (rounded to one decimal) for the low-stressed and high-stressed community. We also determined the average (over all iterations) dissimilarity index (and its components) and the average log transformed abundance ratio per factorial combination and for the low-stressed and high-stressed community separately.

3.3 Results

For the low-stressed community, we found that the proportion of hump-shaped relationships between dispersal and diversity (local richness) was highest at an intermediate stress heterogeneity (Fig. 3.3). Furthermore, for the high-stressed community, the proportion of hump-shaped relationships increased when stress heterogeneity increased (Fig. 3.3). Hence, the proportion of hump-shaped relationships was generally higher for the high-stressed than for the low-stressed community.

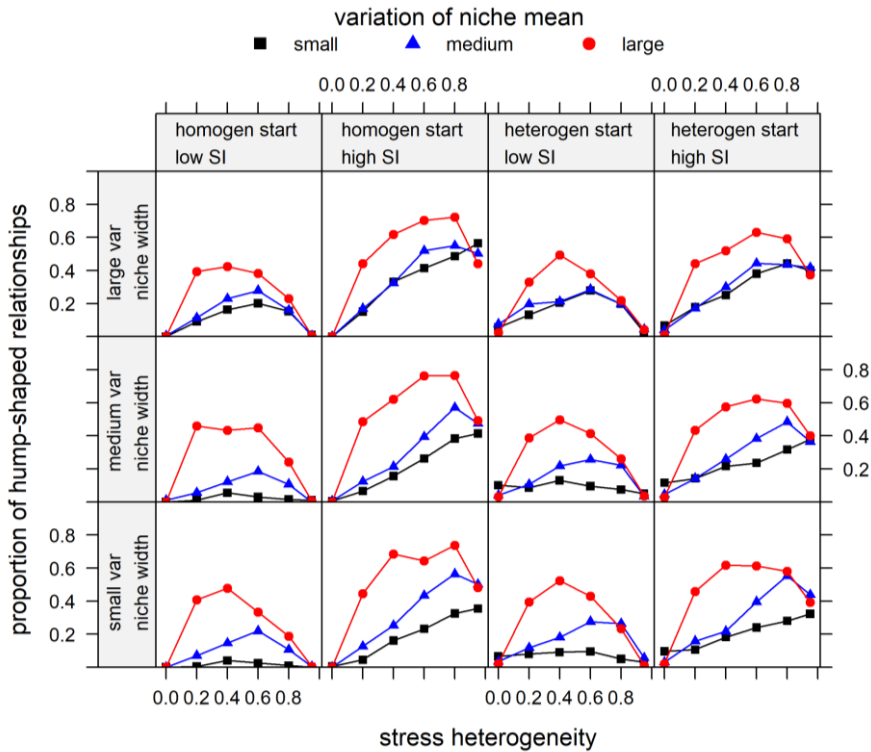


Fig.3.3. Proportion of hump-shaped relationships in function of stress heterogeneity. Abbreviations: homogen start/heterogen start: homogeneous or heterogeneous starting composition; low SI/high SI: low-stressed and high-stressed community; var: variation.

The variation of the niche mean and niche width had a positive effect on the proportion of hump-shaped relationships, and mostly at an intermediate stress heterogeneity. The proportion of hump-shaped relationships increased when the starting composition was heterogeneous, but only when stress heterogeneity was low and the variation of the niche mean was small (Fig. 3.3). As a result, when the starting composition was heterogeneous, hump-shaped relationships also appeared in the absence of stress heterogeneity.

The proportion of positive relationships was lower than the proportion of hump-shaped relationships (Fig. 3.4). For the low-stressed community, the proportion of positive relationships showed similar trends as for the hump-shaped relationships when the starting composition was homogeneous. For the high-stressed community, or when the starting composition was heterogeneous, the effect of stress heterogeneity on the proportion of positive relationships did not show a clear trend. Moreover, the proportion of positive relationships did not depend on the interspecific variation of the stress response. Negative relationships between dispersal and diversity were scarce (Appendix B3 Fig. B3.3).

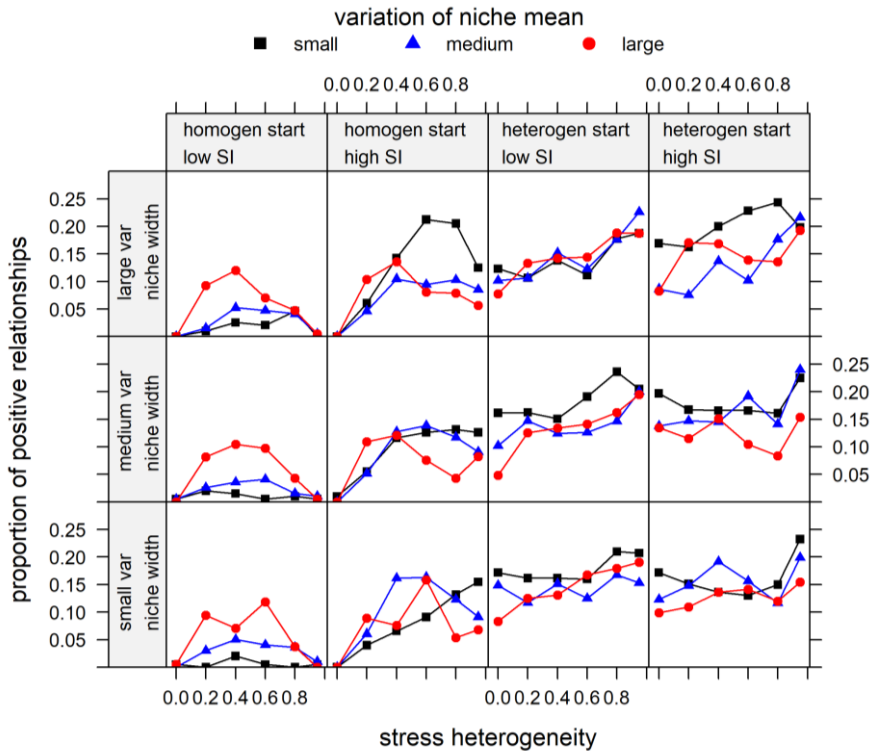


Fig. 3.4. Proportion of positive relationships in function of the stress heterogeneity. Note the other y-axis than in Fig. 3.2. Abbreviations: homogen start/heterogen start: homogeneous or heterogeneous starting composition; small SI/high SI: low-stressed and high-stressed community; var: variation.

The proportion of hump-shaped relationships increased with the dissimilarity in composition between the low-stressed and high-stressed community, but this increase was weaker for the low-stressed than for the high-stressed community (Fig. 3.5). Dissimilarity increased with the magnitude of stress heterogeneity, the variation of the interspecific response to stress and was greater when the starting community composition was heterogeneous. An increasing stress heterogeneity increased the nestedness component of composition dissimilarity (Appendix B3 Fig. B3.4c), and this was mainly due to a lower richness in the high-stressed community (Appendix B3 Fig. B3.5).

For the low-stressed community, the proportion of hump-shaped relationships increased with an increasing abundance ratio between the high-stressed and low-stressed community (Fig. 3.6). For the high-stressed community, the proportion of hump-shaped relationships did not vary in a consistent way with the abundance ratio (Fig. 3.6). A stronger stress heterogeneity increased the abundance ratio between the high- and low-stressed community (Appendix B3

Fig. B3.4). A higher variation of the interspecific response to stress reduced the rate at which the difference in abundance increased when stress heterogeneity increased. Starting composition hardly affected the abundance ratio.

3.4 Discussion

3.4.1 Stress heterogeneity

As expected, we found that the proportion of hump-shaped relationships increased with stress heterogeneity for the high-stressed community, but was highest at an intermediate stress heterogeneity for the low-stressed community (Fig. 3.3). For the high-stressed community, an increasing stress heterogeneity increased the proportion of hump-shaped relationships between dispersal and diversity by increasing dissimilarity in composition between the low-stressed and high-stressed community (Fig. 3.5). This increase in dissimilarity was the results of the different stress intensity among communities which selected for the locally best adapted species (Appendix B3 Fig. B3.4a). Because of these differences in composition, dispersal generated mass effects, increasing local diversity at an intermediate rate by introducing species that were locally excluded and decreasing diversity at a high rate through metacommunity homogenization (Mouquet and Loreau 2003, Mouquet et al. 2006).

For the low-stressed community, the proportion of hump-shaped relationships between dispersal and diversity increased at a low and intermediate stress heterogeneity, but decreased at a high stress-heterogeneity. An increasing stress heterogeneity increased the proportion of hump-shaped relationships between dispersal and diversity because dispersal created mass effects when the dissimilarity in composition between the low-stressed and high-stressed community increased. However, at a high stress heterogeneity, the proportion of hump-shaped relationships was low despite the high dissimilarity in composition (Appendix B3 Fig. B3.4a). Indeed, for the low-stressed community, the proportion of hump-shaped relationships was low, even at a maximal dissimilarity (Fig. 3.5). In contrast, the proportion of hump-shaped relationships for the low-stressed community was strongly affected by the abundance ratio between the high- and low stressed community: the lowest proportion of hump-shaped relationships was found at a low abundance ratio (Fig. 3.6). Stress heterogeneity decreased the abundance ratio between the high- and low stressed community as it strongly decreased the productivity of the high-stressed community while increasing the abundance of the low-stressed community.

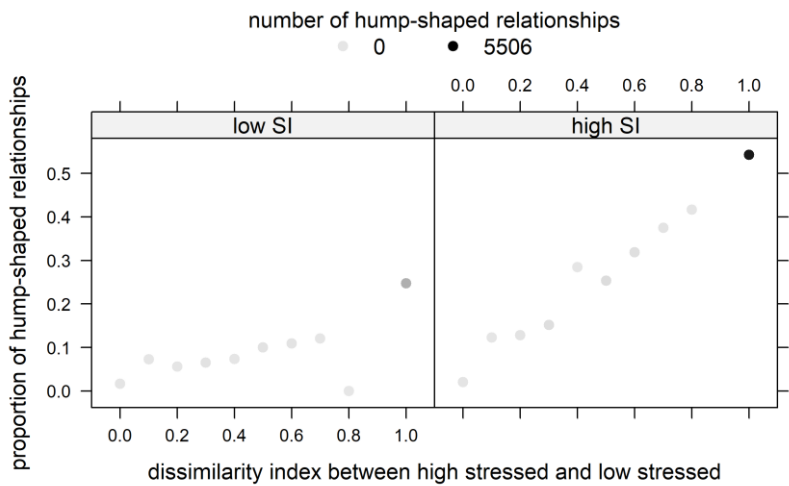


Fig. 3.5. The proportion of hump-shaped relationships as function of the Sørensen dissimilarity index (rounded to one decimal) for the low-stressed and high-stressed community. The gray-values represent the absolute number of hump-shaped relationships at the corresponding dissimilarity index.

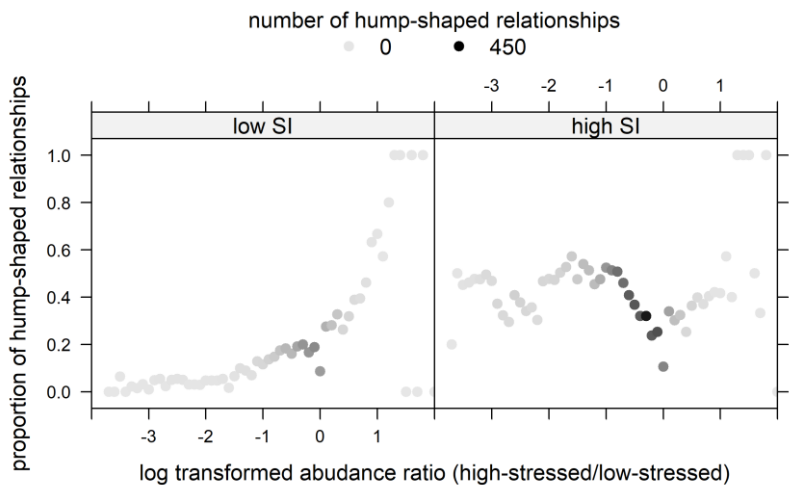


Fig. 3.6. The proportion of hump-shaped relationships as function of the log transformed abundance ratio (high-stressed to low-stressed) (rounded to one decimal) for the low-stressed and high-stressed community. The gray-values represent the absolute number of hump-shaped relationships at the corresponding abundance ratio.

There are two reasons why the proportion of hump-shaped relationships for the low-stressed community was lowest at a low abundance ratio. First, because we manipulated the fraction of dispersed organisms, a high stress intensity reduced the number of organisms that dispersed from the high- to the low-stressed community. Hence, at a high stress heterogeneity, organisms were introduced at a slower rate than they were excluded from the low-stressed community. Therefore, dispersal did not increase diversity and no hump-shaped relationships appeared for the low-stressed community. Second, a high stress heterogeneity increased the nestedness component of dissimilarity, meaning that the number of unique species in the high-stressed community (i.e. species that were not present in the low-stress community) was small (Appendix B3 Fig. B3.4c, Fig. B3.5). The nestedness component increased because the death rate of most species exceeded their birth rate and stochastic extinctions were more likely because of the small population sizes (Eriksson et al. 2013, Huang et al. 2015). When the high-stressed community had little to no unique species, dispersal could not introduce new species to the low-stressed community and as such it did not affect diversity for the low-stress community.

An often considered type of environmental stress is the random removal of organisms. These random removals reduce the average growth rate of the populations, independent of species identity. Therefore, the effect of random removals is similar to our model scenario where the variation of the niche optimum and niche width were small, i.e. all species are – on average – equally sensitive. Altermatt et al. (2011) investigated the effect of dispersal (absence vs. presence) in metacommunities where patches were exposed to different levels of random removals. While dispersal did not affect local richness in the undisturbed patches, dispersal increased diversity in the disturbed patches. This is consistent with our results showing that the proportion of positive or hump-shaped relationships is higher for a high-stressed than for a low-stressed community.

3.4.2 Interspecific variation in stress response

As expected, more hump-shaped relationships appeared at a higher interspecific variation of the niche mean and the niche width. This was due to a more rapid species turnover, and therefore a more rapid increase of composition dissimilarity when stress heterogeneity increased (Appendix B3 Fig. B3.4a).

Our study indicates that the relationship between dispersal and diversity can only emerge when the environmental conditions affect species differently among patches. However, data on how species respond to local environmental conditions are often not included in studies testing the influence of dispersal on local diversity. In the few studies that include such information, no hump-shaped relationship was found. In the study of Matthiessen et al. (2010),

for instance, stress heterogeneity was low (approximately 5%, based on the growth rate of the most abundant algae strains) and species showed similar sensitivities towards a change of the environmental conditions. Our results indeed suggest that under such conditions the probability to find a hump-shaped relationship between dispersal and diversity is low. In contrast, Limberger et al. (2014) applied a stress heterogeneity of 35% by applying a temperature gradient (based on the ratio of the average growth rate at a low and high temperature). Species showed a different sensitivity towards the temperature change which resulted in the exclusion of one species at the highest temperature. According to our results, these conditions have a high probability to generate a hump-shaped relationship. A possible reason why Limberger et al. (2014) did not find a hump-shaped relationship was that dispersal was probably too weak to generate mass effects. Also, they applied only two dispersal levels, which are too few to find a hump-shaped relationship. In general, there is still a lack of studies that apply a strong stress heterogeneity. Therefore, it is not possible to thoroughly validate our theoretical results empirically. Moreover, it should be noted that in the studies of Matthiessen et al. (2010) and Limberger et al. (2014), stress heterogeneity hardly affected richness. A possible reason for this is that competitive exclusion took longer than the experiment duration and that species were not yet at their equilibrium density at the end of the experiment (Hillebrand et al. 2008). This might explain why so few hump-shaped relationships were found in experiments (Grainger and Gilbert 2016), while they are often predicted by models (Mouquet and Loreau 2003, Loreau et al. 2003a, Gilbert 2012).

3.4.3 Heterogeneity in starting composition

As expected, a heterogeneous starting composition increased the proportion of hump-shaped relationships between dispersal and local richness and, to a lesser extent, the proportion of negative relationships. Even without stress heterogeneity, a heterogeneous starting composition created a high dissimilarity among the communities because some species were initially present in one community, but not in the other (Appendix B3 Fig. B3.4a). Such differences in composition are common in empirical metacommunity experiments, when communities are composed of species drawn from natural communities, pooled sources or natural colonization. These differences might be generated stochastically, as in our study, or by historical processes such as priority effects.

When starting compositions are heterogeneous, positive relationships between dispersal and local richness appeared because of two reasons. First, dispersal may increase diversity by introducing dispersal-limited species, which did not occur when the starting composition was homogeneous. Second, dispersal can increase diversity by keeping weak competitors in patches. Hump-shaped relationships might then appear when a high dispersal rate enables the regional dominant competitor to invade each community, excluding subdominant species.

Such hump-shaped relationships have been found in several experiments with heterogeneous starting compositions (Cadotte 2006, Matthiessen and Hillebrand 2006, Kneitel and Miller 2011). However, in some of these studies, the hump-shaped relationship might have been the result of competition-colonization trade-offs (Cadotte 2006, Matthiessen and Hillebrand 2006), which were not considered in our simulations. We also found that dispersal often increased diversity, without homogenizing the metacommunity at a high dispersal rate. Consistent to our theoretical results, many empirical studies that used heterogeneous compositions found positive relationships between dispersal and diversity, even when environmental conditions were homogeneous (e.g. Gilbert et al. 1998, Gonzalez et al. 1998, Cadotte and Fukami 2005, Öslman et al. 2006). Nevertheless, dispersal did not always increase diversity by introducing dispersal-limited species. When dispersal introduced competitive dominant species, these species could just replace the resident species, keeping diversity constant or even reducing diversity. The fact that dispersal might not always affect diversity is confirmed in several empirical studies (e.g. Hoyle and Gilbert 2004, France and Duffy 2006, Limberger and Wickham 2012).

When stress heterogeneity increased, the proportion of hump-shaped relationships was higher for the high-stressed than for the low-stressed community (Fig. 3.3). This seems consistent to Matthiessen et al. 2010b who found no hump-shaped relationships in communities without disturbances but found that hump-shaped relationships appear in communities where disturbances were applied.

When the interspecific variation of the niche mean and niche width were high, the proportion of hump-shaped relationships was similar for homogeneous and heterogeneous starting composition. Studies that manipulate environmental heterogeneity in communities with a heterogeneous starting composition, are scarce and they do not report species sensitivities or differences in stress intensity. Pedruski and Arnott (2011) found a positive relationship between dispersal and diversity in both homogeneous and heterogeneous environments where substrate heterogeneity was applied. In contrast, Chisholm et al. (2011) found that heterogeneity (wet versus dry patches) can generate a positive relationship between dispersal and diversity, while there was none in a homogeneous environment. Last, Forbes and Chase (2002) did not find any effect of nutrient heterogeneity on the relationship between dispersal and diversity as the relationship was never significant. Empirical studies thus show a high variation in relationships, which is in line with our results. However, due to a lack of empirical data it is not possible to experimentally validate our theoretical results for the different factor combinations.

3.4.4 The influence of dispersal rate and interaction coefficients

In the present study, the total of positive, negative and hump-shaped relationships was below 100% for all parameter combinations because the relationship between dispersal and diversity was often flat or showed a complex pattern with multiple local maxima. The relationship between dispersal and diversity was not only regulated by the factor combinations that were considered in this study (stress heterogeneity, interspecific variation in stress response, starting composition) but also by other factors and parameters. The per-capita interaction coefficients are an important determinant of the relationship between dispersal and diversity by regulating composition. The stronger the differences in competitive strength among species, the higher the variations in stress response must be to create different compositions. Moreover, when the strongest competitor is also the most stress-tolerant species, stress heterogeneity might generate no differences in composition (De Laender et al. 2016).

Interaction coefficients are demonstrated to influence if the relationship between dispersal and diversity is hump-shaped or positive (Amarasekare and Nisbet 2001). In particular, hump-shaped relationships occur when a strong regional competitor excludes subdominant species at a high dispersal rate (Mouquet and Loreau 2003). However, this exclusion does not occur under global niche partitioning when none of the species is a regional superior competitor (Amarasekare and Nisbet 2001). In that case, the relationship between dispersal and diversity might be positive. It is very likely that for certain combinations of interaction coefficients global niche partitioning occurs, which explains the relatively high proportion of positive relationships between dispersal and diversity.

According to the stress gradient hypothesis, an increasing stress-intensity decreases competitive interactions while increasing facilitative interactions (Grime 1973, Maestre et al. 2009). However, the stress gradient hypothesis is debated (Chesson and Huntly 1997). Moreover, Baert et al. (2016) did not find any stressor-induced changes in per-capita interaction coefficients in communities of micro-algae, the model organisms that we used. Therefore, we did not alter the per-capita interaction coefficients along the stress-intensity gradient in this study.

While we tested a broad range of parameter values, we strongly controlled the dispersal rate as we did not allow for unequal dispersal probabilities among species and dispersal was asymmetric. Nevertheless, asymmetric dispersal of a competitive dominant species increases the probability for coexistence and thus for positive or hump-shaped relationships (Salomon et al. 2010, Haegeman and Loreau 2015). However, theoretical and experimental work on asymmetric dispersal is still scarce and should be performed in the future.

3.4.5 Conclusion

Many communities today are exposed to environmental stress. These stressors are known to create shifts in composition and species abundances. We showed that these shifts can influence the shape of dispersal-diversity relationships, conditional on the local stress-intensity level, interspecific variation in stress response and the starting composition. Based on our theoretical results, we argue that empirical studies are needed to investigate the relationship between dispersal and diversity under stress. Moreover, these studies need to include information about the extent to which stress affects both the composition and species abundances to assess the results thoroughly.

4

The relationship between beta-diversity and regional productivity along a stressor flux gradient

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Abstract.

Dispersal of organisms can influence the relationship between beta-diversity and regional productivity in heterogeneous environments. However, many ecosystems are also linked by fluxes of stressors, with an unknown influence on this relationship. In this study, we assess the relationship between beta-diversity (measured as Bray-Curtis dissimilarity) and regional productivity (measured as biovolume) under various levels of a stressor flux in meta-ecosystems that were composed of two marine micro-algae communities. We created heterogeneity by exposing one of the two communities to a herbicide and manipulated regional diversity by applying a dispersal gradient, which decreased beta-diversity. We applied four stressor flux levels, which homogenized the herbicide concentration between the communities over time. The stressor flux changed the relationship between beta-diversity and regional productivity by changing the effect of dispersal on regional productivity. In absence of the stressor flux, the relationship between beta-diversity and regional productivity was positive at the end of the experiment. This positive relationship was generated by a negative effect of dispersal on regional productivity, probably because dispersal disrupted local dynamics by removing organisms from the most-productive unstressed community. In presence of the stressor flux, the relationship between beta-diversity and regional productivity was often negative as dispersal now increased regional productivity. Dispersal increased regional productivity by increasing the productivity of the stressed community. This positive effect was stronger in the presence than in the absence of the stressor flux because the stressor flux reduced the concentration of the herbicide in the stressed community, where it facilitated recovery. Our study shows that stressor fluxes can strongly interact with the effects of dispersal on productivity and thus influence diversity-productivity relationships.

4.1 Introduction

Stressors such as global warming, habitat fragmentation or the release of chemical stressors are changing global biodiversity (Vörösmarty et al. 2010, Malaj et al. 2014, Pimm et al. 2014). To date, both theoretical and field studies have provided ample evidence that biodiversity changes affect ecosystem provisioning in closed systems, and that the consequences of biodiversity changes are altered by stressors (Cardinale et al. 2012, Hooper et al. 2012, Tilman et al. 2014, De Laender et al. 2016, Baert et al. 2018). However, a major open challenge is to unravel how biodiversity and ecosystem functioning are related at a regional scale. Meta-ecosystems are ecosystems in which spatial fluxes of organisms (dispersal), energy and materials are explicitly considered (Loreau et al. 2003b, Massol et al. 2011). Those fluxes can change regional and local diversity, ecosystem functioning (e.g. productivity) and the relationship between both (Loreau et al. 2003b, Haegeman and Loreau 2014, Leibold et al. 2017, Massol et al. 2017).

A well-known component of diversity is beta-diversity, which quantifies the difference in community composition (Whittaker 1960). In heterogeneous environments, differences in composition among communities are mainly generated by local competitive processes (Cottenie 2005, Myers et al. 2015). Many studies have found a positive relationship between beta-diversity and regional productivity (Chase and Leibold 2002, Chalcraft et al. 2004, Chase and Ryberg 2004, Harrison et al. 2006). One possible mechanism for such a positive relationship is that dispersal reduces both beta-diversity and regional productivity. Dispersal might reduce beta-diversity for two reasons. First, dispersal can decrease the differences in species densities among communities (Baselga 2013, Gianuca et al. 2016). Second, dispersal can introduce new species from other communities or maintain species in communities where they would otherwise be excluded through competition (Mouquet and Loreau 2003, Baselga 2013). The latter occurs in source-sink communities in which organisms disperse from communities where they are strong competitors (the source), to communities where they are weak competitors (the sink) (Leibold et al. 2004). Dispersal might reduce regional productivity in source-sink communities (Mouquet and Loreau 2003, Leibold et al. 2017) because dispersal can move organisms from communities where they are locally adapted (and therefore highly productive) to communities where they are less adapted (and therefore less productive) (Mouquet and Loreau 2003). Negative dispersal effects on productivity mostly appear at high dispersal rates (Howeth and Leibold 2010a, Lindström and Östman 2011), but have also been found at low dispersal rates in micro-algae communities (Eggers et al. 2012, de Boer et al. 2014).

Next to a negative effect on regional productivity, dispersal might also increase regional productivity by maintaining diversity under changing environmental conditions, also referred to as the spatial insurance effect (Loreau et al. 2003a, Steiner et al. 2011, Symons and Arnott 2013, de Boer et al. 2014). Fluxes of materials, such as resources and chemical stressors, can generate spatiotemporal changes of environmental conditions, and can interfere with the effect of dispersal on diversity and productivity on a regional scale (Loreau et al. 2003b, Massol et al. 2011, Haegeman and Loreau 2014). However, empirical studies that combine dispersal and material fluxes are generally lacking (Massol et al. 2017). Moreover, to test how dispersal and material fluxes interact, there is a need for studies that manipulate dispersal and material fluxes independently (Massol et al. 2017). To our knowledge, so far only one study has done so, finding dispersal and a resource flux to increase ecosystem functioning (Harvey et al. 2016). However, it is unsure to what extent these results apply to other kinds of material fluxes. Indeed, organisms can produce or consume resources (Staddon et al. 2010, Harvey et al. 2016), while they are generally not able to impact environmental stressors such as pesticides (Chase and Leibold 2003).

This study independently manipulates dispersal and the flux of a chemical stressor to investigate how both factors combine in affecting the relationship between beta-diversity and regional productivity. We used heterogeneous two-patch meta-ecosystems, in which both patches initially contained an identical micro-algae community. Within each meta-ecosystem, heterogeneity was created by initially exposing only one community to the photosynthesis inhibiting pesticide atrazine. This stressor reduced the growth of the micro-algae in a species-specific way and therefore induced a different composition in the unstressed (no stressor present on day 0) than in the stressed (stressor present on day 0) community. We manipulated dispersal over the two-patch meta-ecosystems by moving a fixed proportion of algae between the unexposed and exposed community, homogenizing the composition and installing a gradient in beta-diversity. Next, we simulated a stressor flux (four levels) within the meta-ecosystems. Because of this stressor flux, the stressor concentration increased in the unstressed community and decreased in the stressed community.

Regardless of the stressor flux level, we expected that dispersal would reduce beta-diversity (Mouquet and Loreau 2003), creating a beta-diversity gradient. In the absence of the stressor flux we expected to find a positive relationship between beta-diversity and regional productivity, as found in earlier studies (e.g. Chase and Leibold 2002) (Fig. 4.1). This relationship is expected to appear because dispersal would decrease regional productivity by disrupting local community processes, as theoretically predicted by Mouquet and Loreau (2003) and experimentally found in other marine micro-algae communities (Eggers et al. 2012, de Boer et al. 2014). Conversely, in the presence of the stressor flux, we predicted that

dispersal would increase regional productivity by introducing better-adapted organisms in communities where the stressor concentration was changed by the stressor flux, generating a negative relationship between beta-diversity and regional productivity (Fig. 4.1). Thus, overall, we expected the stressor flux to change the relationship between beta-diversity and regional productivity from positive (without flux) to negative (with flux).

We performed additional analyses to investigate how the stressor flux influenced the relationship between beta-diversity and regional productivity. First, we investigated the effect of dispersal on beta-diversity and on community composition (the density of the dominant algae strains). Second, we examined how dispersal changed regional and local productivity for the various stressor flux levels. Last, we also assessed the sensitivity of the dominant algae strains towards the stressor.

4.2 Materials and methods

4.2.1 Algae strains

Marine diatoms (*Bacillariophyceae*) were collected from the Belgian part of the Southern Bight of the North Sea with a 10 μm mesh size phytoplankton net. We isolated individual algae cells following the protocol of Andersen and Kawachi (2005). Each algae cell thus gave rise to a monoclonal algae culture, indicated as *strain*. The algae strains were identified to the genus level using a light microscope and cell volumes were calculated according Hillebrand et al. (1999) (Supplementary Material Appendix A1, Table A1). They were grown in f/2 medium (Guillard and Ryther 1962) composed of artificial seawater (Instant Ocean®, Aquarium Systems) supplemented with 30 mg l^{-1} silicon and kept in a climate room ($20 \pm 1^\circ\text{C}$) with a 16h photoperiod at $35 \pm 5 \mu\text{mol photons m}^{-2}\text{s}^{-1}$ light intensity (Lumilux® Coolwhite, Osram). New cultures were inoculated every week to keep the cultures in the exponential or early stationary growth phase. From the available stock cultures, six cultures were randomly selected for the experiment. Each culture contained organisms of a different genus: *Navicula* sp., *Thalassiosira* sp., *Odontella* sp., *Asterionellopsis* sp., *Asterionella* sp. and *Melosira* sp. In this manuscript, these genera will hereafter be indicated as “strain”.

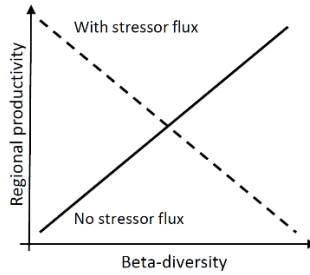


Fig. 4.1. Hypothesized relationship between beta-diversity and regional productivity in the absence or the presence of the stressor flux.

4.2.2 Experimental design

Each experimental meta-ecosystem consisted of two local patches that contained micro-algae grown in individual Erlenmeyer flasks at two different concentrations of the chemical stressor atrazine (unstressed: $0 \mu\text{g l}^{-1}$ and stressed: $250 \mu\text{g l}^{-1}$) to create stressor heterogeneity. At the start of the experiment, the six algae strains were added together in f/2 medium at an equal abundance of $5 \times 10^7 \mu\text{m}^3$ per strain to achieve a final culture volume of 30 ml per flask. We used a full factorial design with 4 stressor flux levels (0%, 5%, 10% and 15%, see below) and 5 dispersal levels (0%, 5%, 10%, 15% and 20%, see below). The stressor flux and dispersal were manipulated on the same day, every 4 days. All treatments were replicated 3 times, obtaining 60 two-patch meta-ecosystems. The experiment ran for 24 days.

At a stressor flux of x%, we simulated every four days the exchange of x% of medium containing the stressor between the unstressed and stressed community (Fig. 4.2). Hence, the concentration of the stressor in the unstressed community increased and the concentration of the stressor in the stressed community decreased, while the total amount and the mean concentration of the stressor across the meta-ecosystem remained constant (Appendix C, Fig. C1). We simulated the exchange of the stressor by removing old and adding new medium, manipulating the stressor concentration. To manipulate the stressor concentration, 10 ml of culture was centrifuged (Fig. 4.2) and 9 ml of supernatant was removed and stored for nutrient and atrazine analysis. The residue, containing the algae, was added back to the culture. Next, 10 ml of new medium was added to the flask. The atrazine concentration of the added medium depended on the stressor flux rate. The added medium had the appropriate atrazine concentration to obtain the same concentration as if the medium would have been directly exchanged between flasks (Appendix C, Table C2a-C2c). By adding new medium, we made sure that only the stressor was manipulated but no other compounds in the water, such as nutrients. Appendix C, Tables C2a, C2b, C2c provide the values of theoretical concentration of the stressor in the medium after a stressor flux, the concentration

of stressor in the added medium, and the measurements of the stressor concentrations at the end of the experiment (mean concentration of the three replicates within the no-dispersal treatment). Our measurements show small deviations between the predicted and measured concentrations and confirmed that a higher stressor flux increased the concentration in the unexposed communities, while reducing the concentration in the exposed communities. However, the flux did not completely homogenize the stressor concentration by the end of the experiment. The average concentration within each meta-ecosystem was always close to $125 \mu\text{g l}^{-1}$ along all stressor flux levels. The added medium was not added directly to the flasks because the medium was used to rinse the centrifuge tubes to avoid any algae loss. 5 ml was used to rinse the centrifuge tube during the stressor flux phase, and 5 ml was used to rinse the centrifuge tube during the dispersal phase (see below).

Next to the replacement of medium during the stressor flux, we also renewed medium two days after the manipulation of the stressor flux (days 2, 6, 10, 14, 18 and 22). Medium replacement was done for two reasons. First, atrazine had to be replaced regularly because it is degraded by light (half-life value between 90-120 days (Solomon et al. 1996)). By replacing the medium, the atrazine concentration mostly changed because of the simulated stressor flux rather than because of degradation. Second, medium replacement delayed nutrient depletion. Medium replacement was done by removing 10 ml from the upper layer of the culture (diatoms tend to sink to the bottom of the flask), followed by the addition of 10 ml of clean medium at the original atrazine concentration and manual shaking of the flasks.

Dispersal was manipulated together with the stressor flux by moving a fixed proportion of the algae between the two patches of each meta-ecosystem (Fig. 4.2). First, a flask was shaken to homogenize the algae cultures. Next, we pipetted 0%, 5%, 10%, 15% or 20% of each culture into a 8 ml centrifuge tube. After centrifugation, the supernatant was added back to the original flask, after which only 0.2 ml of the residue remained in the centrifuge tube. Because the algae and medium cannot be completely separated, we rinsed the algae with new medium that had the same concentration as the flask where the algae dispersed to. To remove the rinsing medium, the tube was centrifuged again, after which the supernatant was removed until 0.2 ml of residue remained. After adding the residue to the target flask, the centrifuge tube was rinsed with 5 ml of medium, which had the appropriate concentration to reach the target concentration, to avoid any algae loss (see above). This rinsing medium was then also added to the target flask.

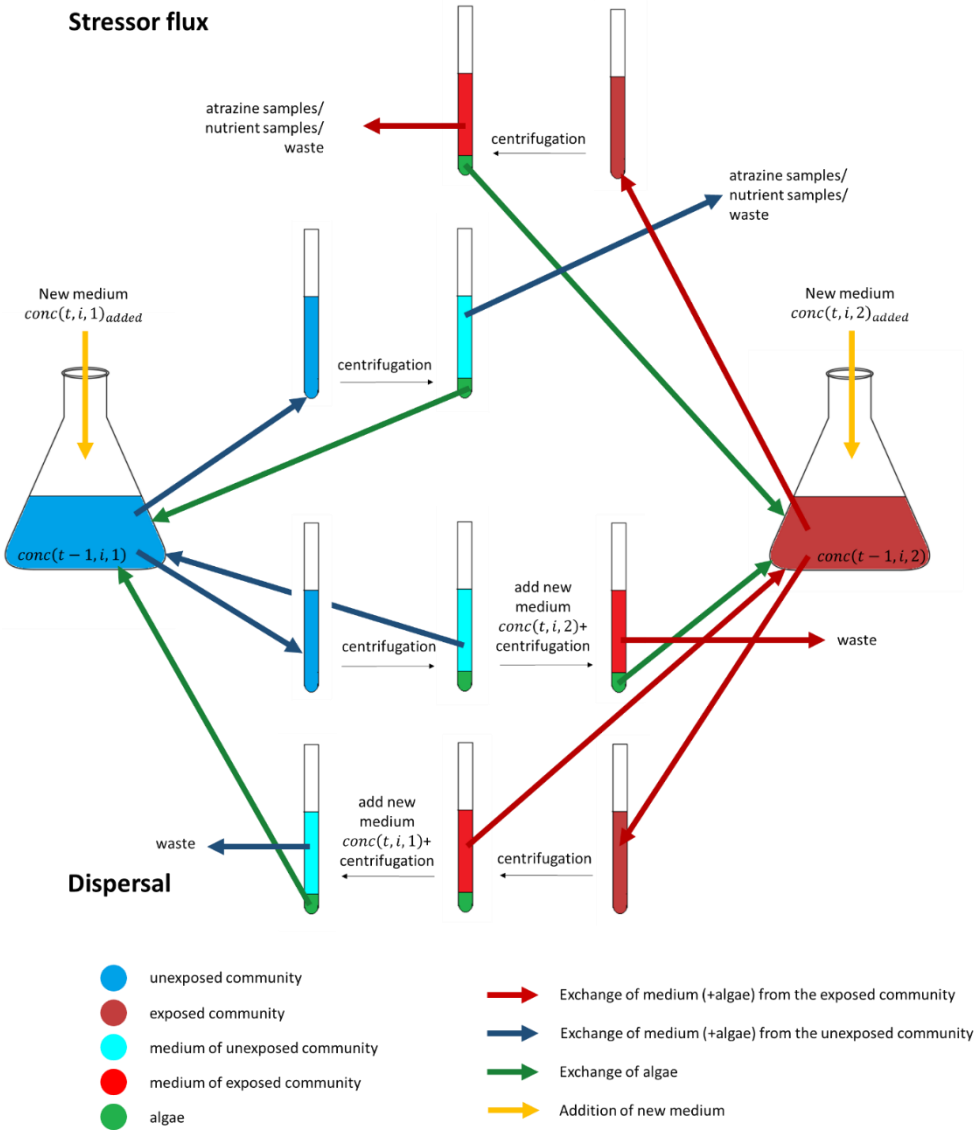


Fig. 4.2. Manipulation of the stressor flux and dispersal between an unexposed (blue) and exposed community (red). The stressor flux and dispersal were performed on days 4, 8, 12, 16 and 20. Thick arrows represent a manipulation that was performed by pipetting algae and/or medium. $conc(t, i, j)_{added}$ is the concentration of the added medium; $conc(t, i, j)$ is the target concentration of the medium. For clarity, the rinsing of the centrifuge tubes is not shown in the figure.

All cultures were grown in a climate room (20 ± 1 °C) under $35 \pm 5 \mu\text{mol photons } m^{-2} s^{-1}$ light intensity at a 16h photoperiod. Erlenmeyer flasks were repositioned every 2 days to eliminate

potential differential light effects in the climate room. Every 4 days, just before manipulating the stressor flux and dispersal, we took 1 ml samples for algae counting. The samples thus show the state of the communities 4 days after the most recent manipulation of the stressor flux and dispersal. The samples were conserved with 0.2 ml of formaldehyde (35%) and stored at 4°C in 24 multiwell-plates for conservation. From each sample, a subsample was counted using an inverse microscope and Whipple grid. The size of the subsample depended on the cell density, but was sufficient to always include more than 100 cells of the most dominant strain. Nutrient samples were stored at 4°C and analyzed by Spectroquant® spectrophotometry (Appendix C, Table C3). Atrazine concentrations were determined using HPLC (Appendix C, Table C2a, C2b, C2c).

Before the meta-ecosystem experiment, we determined the algae growth parameters and sensitivity to the chemical stressor in monoculture at 5 different concentrations of the chemical stressor atrazine (Sigma Aldrich) (0, 50, 100, 250, 500 $\mu\text{g l}^{-1}$). Algae were grown during 14 days in Erlenmeyer flasks under the same conditions as the two-patch experiment. Cell densities were determined at day 4, 7, 9, 11, and 14 from 1 ml samples using a Whipple Grid.

4.2.3 Data analysis

We quantified beta-diversity by measuring Bray-Curtis dissimilarity, using the betapart package in R (Baselga et al. 2013). Because of the variability in cell sizes among strains, Bray-Curtis dissimilarity was determined using the individual strains' biomass calculated as biovolume (Hillebrand et al. 1999). As a measure of productivity, we used total biovolume. For the statistical analyses, biovolumes were log transformed to obtain normality of the residuals.

The effects of beta-diversity, the stressor flux and time on the log transformed regional productivity were determined using Eq. 4.1

$$\begin{aligned}
 \log \text{ regional productivity}_i &= \alpha + \beta_1 * \text{beta diversity}_i + \beta_2 * \text{stressor flux}_i + \beta_3 \\
 &* \text{time}_i + \beta_4 * \text{time}_i^2 + \beta_5 * \text{beta diversity}_i * \text{stressor flux}_i \\
 &+ \beta_6 * \text{beta diversity}_i * \text{time}_i + \beta_7 * \text{beta diversity}_i * \text{time}_i^2 \\
 &+ \beta_8 * \text{stressor flux}_i * \text{time}_i + \beta_9 * \text{stressor flux}_i * \text{time}_i^2 \\
 &+ \varepsilon_i
 \end{aligned} \tag{Eq. 4.1}$$

With α the estimated intercept of the linear model, and $\beta_1 \dots \beta_9$ the estimated slopes of the linear model. As data are temporally correlated, the correlation cor between the model residuals ε_i and ε_j is given by:

$$cor(\varepsilon_i, \varepsilon_j) = \begin{cases} 1 & \text{if } i = j \\ \rho & \text{else} \end{cases} \quad (\text{Eq. 4.2})$$

The addition of $time_i^2$ as a predictor variable was based on the regional productivity data - model prediction plot (Appendix C Fig. C2).

The effect of dispersal, the stressor flux and time on the log transformed local productivity, as well as on the log transformed density of *Navicula* sp. and *Asterionellopsis* sp. was calculated using Eq. 4.3. Analyses were performed for the unstressed and stressed community separately.

$$\begin{aligned} \log \text{ local productivity}_i &= \alpha + \beta_1 * distance_i + \beta_2 * stressor \text{ flux}_i + \beta_3 * time_i + \beta_4 \\ &* time_i^2 + \beta_5 * distance_i * stressor \text{ flux}_i + \beta_6 * distance_i \\ &* time_i + \beta_7 * distance_i * time_i^2 + \beta_8 * stressor \text{ flux}_i \\ &* time_i + \beta_9 * stressor \text{ flux}_i * time_i^2 + \varepsilon_i \end{aligned} \quad (\text{Eq. 4.3})$$

With α the estimated intercept of the linear model, and $\beta_1 \dots \beta_9$ the estimated slopes of the linear model. As data are temporally correlated, the correlation cor between the model residuals ε_i and ε_j is given by Eq. 4.2.

Model selection was done using the protocol of Zuur et al. (2009) by comparing nested models using the ANOVA test in R (R. Core Team 2016). First, we added an exponential variance structure for the predictor variables, but only when this variance structure significantly increased model performance ($p < 0.1$). Second, we added a temporal correlation structure using the `corCompSymm` function in R (Eq. 4.2). Last, we removed the interactions terms that did not increase model performance using the backward selection method ($p > 0.1$). Model validations are represented in Appendix C Fig. C2-C9. All calculations were done using the `gls` function in R (R. Core Team 2016).

To test for the effect of dispersal on beta-diversity, we fitted a beta-regression model, which is used when the dependent variable is a proportion between 0 and 1. We used dispersal as the predictor variable and the Bray-Curtis dissimilarity as the response variable by using the `betareg` package in R (Cribari-neto and Zeileis 2010). To measure the significance of the predictor variables, the `betareg` package uses the z-statistic, which is the regression coefficient divided by its standard error.

The growth rate (μ) and carrying capacity (K) of the six strains were determined by fitting a logistic growth curve to the monoculture data. The best model fit was calculated by minimizing the sum of squared errors with a simulated annealing algorithm using the `GenSA` package in

R (Xiang et al. 2013). A log-logistic dose-response curve (Eq. 4.4) was fitted to model the effect of atrazine on the per-capita growth rate and carrying capacity using the drc package in R (Ritz et al. 2015)

$$f(conc) = \left(\frac{max}{1 + e^{s(\ln(conc) - \ln(EC_{50}))}} \right) \quad (\text{Eq. 4.4})$$

With $f(conc)$ the growth rate (μ) or carrying capacity (K) as a function of the concentration of the chemical stressor $conc$ ($\mu g\ l^{-1}$), max ($\mu g\ l^{-1}$) the maximum value of the logistic function, s the slope of the dose response curve and EC_{50} ($\mu g\ l^{-1}$) the concentration at which the growth rate or carrying capacity is reduced with 50%. All calculations were performed in R (R. Core Team 2016).

4.3 Results

4.3.1 The relationship between beta-diversity and regional productivity

Beta-diversity significantly increased regional productivity and its effect was strongest at the end of the experiment (Table 4.1). This resulted in a strong positive relationship between beta-diversity and regional productivity in the absence of the stressor flux on day 24 (Fig. 4.3). We also found a negative interaction effect between beta-diversity and the stressor flux (Table 4.1). Therefore, negative relationships appeared in the presence of the stressor flux (Fig. 4.3). These negative relationships appeared first at the highest stressor flux and later also at a low and medium stressor flux level (Fig. 4.3).

Table 4.1. Results of the linear mixed model of the log transformed regional productivity as response variable and beta-diversity, stressor flux, dispersal, time, time² and their interactions as predictor variables. Model selection was based on the backward selection protocol of Zuur et al. (2009) using an ANOVA test. Significance levels: * p<0.05, ** p<0.01, *** p<0.001.

	Estimate	SD	t-value
Intercept	9.142	0.069	132.16***
Beta-diversity	0.691	0.091	7.58***
Stressor flux	1.749	0.0415	4.22***
Time	0.137	0.014	9.52***
Time ²	-0.006	0.001	-7.67***
Beta-diversity x stressor flux	-2.651	0.604	-4.39***
Beta-diversity x time	-0.145	0.021	-7.02***
Beta-diversity x time ²	0.008	0.001	6.45***
Stressor flux x time ²	0.004	0.001	3.25**

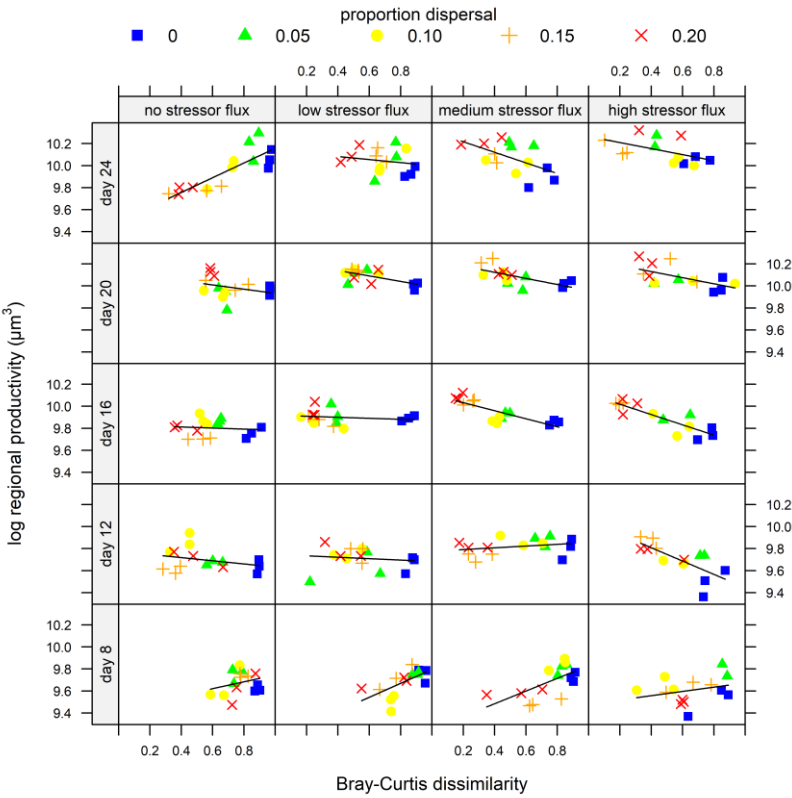


Fig. 4.3. The log transformed regional productivity as function of beta-diversity (Bray-Curtis dissimilarity) between days 8 and 24 for the four stressor flux levels. Symbols represent the data, lines depict the regression lines based on linear models. Samples were taken just before the stressor flux and dispersal were manipulated.

4.3.2 The effect of dispersal on beta-diversity and strain abundances

The presence of the stressor strongly decreased the density of *Asterionellopsis* sp. and *Navicula* sp. in the stressed community (i.e. the community where the stressor was initially present) (Fig. 4.4), generating a high beta-diversity in the meta-ecosystems without dispersal. Dispersal reduced beta-diversity across all stressor flux levels (Fig. 4.4, Appendix C, Table C4) by decreasing the difference in density of the strains between the unstressed and stressed community (Fig. 4.4). We found that dispersal increasingly reduced the abundance of *Navicula* sp. in the unstressed community over time (Appendix C, Table C5). Also the stressor flux reduced the abundance of *Navicula* sp. in the unstressed community, and this effect was strongest at intermediate time steps and in the absence of dispersal (Fig. 4.4, Appendix C, Table C5). In the stressed community, dispersal and the stressor flux increased the density of *Asterionellopsis* sp. and *Navicula* sp. at all stressor flux levels (Fig. 4.4, Appendix C, Table C5, C6). Because of a positive interaction effect between dispersal and the stressor flux, dispersal increased the density of *Navicula* sp. more in the presence than in the absence of the stressor flux (Table C5).

4.3.3 The effect of dispersal on local productivity

We found a significant interaction effect between dispersal and time² (Table 4.2). Therefore, negative relationships between dispersal and the local productivity of the unexposed community appeared at the end of the experiment (Fig. 4.5). However, we found a positive interaction effect between dispersal, stressor flux and time (Table 4.2), and negative relationships between dispersal and the local productivity in the unstressed community were hence weak or absent in the presence of the stressor flux (Fig. 4.5).

Dispersal significantly increased local productivity of the exposed communities and its effect increased in time (Table 4.2). This resulted in a positive relationship between dispersal and local productivity in the stressed community across all stressor flux levels during the entire experiment (Fig. 4.5). We also found a significant negative interaction effect between dispersal, stressor flux and time². However, because the stressor flux increased the log transformed local productivity of the exposed communities (Table 4.2), the effect of dispersal on the local productivity of the stressed community on an absolute scale was stronger in the presence than in the absence of the stressor flux (Fig. 4.5).

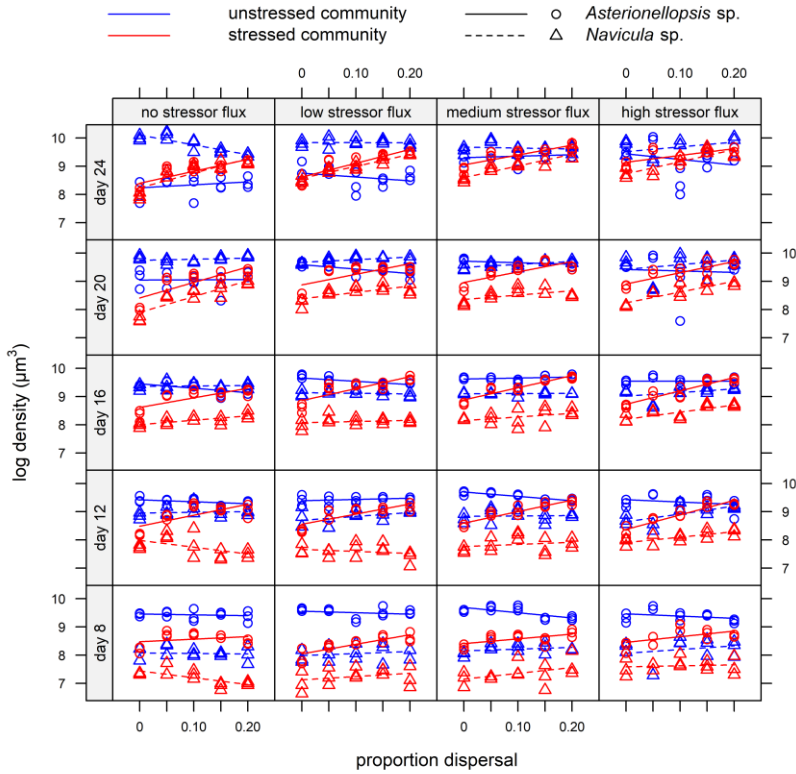


Fig. 4.4. The log transformed local density of *Asterionellopsis* sp. (circle) and *Navicula* sp. (triangle) in the unexposed (blue) and exposed (red) communities as function of dispersal between days 8 and 24 for the four stressor flux levels. Symbols represent the data, lines depict the regression lines based on linear models. Samples were taken just before the stressor flux and dispersal were manipulated.

4.3.4 Strain sensitivities

Asterionellopsis sp. and *Navicula* sp. greatly influenced community dynamics, as they together accounted for more than 90% of the total biovolume in the unstressed and stressed community (day 24 - no stressor flux, no dispersal treatment) (Fig. 4.6, Appendix C, Fig. C7). A monoculture bioassay showed that the growth rate of these two dominant strains had a similar sensitivity to the chemical stressor, while the carrying capacity of *Asterionellopsis* sp. was less sensitive than that of *Navicula* sp. (Fig. 4.6, Appendix C, Table C1).

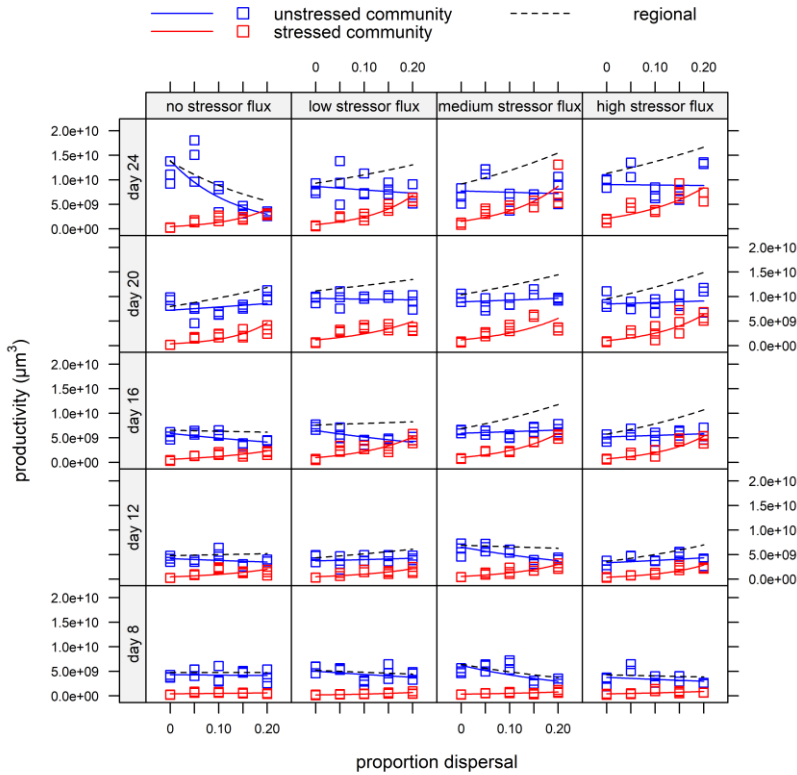


Fig. 4.5. The log transformed local productivity in the unexposed (blue) and exposed (red) communities as function of dispersal between days 8 and 24 for the four stressor flux levels. Symbols represent the data, lines depict the regression lines based on linear models. The black dashed line represents the effect of dispersal on regional productivity. Data of regional productivity are not shown for clarity. Samples were taken just before the stressor flux and dispersal were manipulated.

Table 4.2. Results of the linear mixed effect model of the log transformed local productivity of the unexposed (left) and exposed (right) communities as response variable and dispersal, stressor flux, dispersal, time, time² and their interactions as predictor variables. Model selection was based on the backward selection protocol of Zuur 2009 using an ANOVA test. Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Unexposed community			Exposed community		
	Estimate	SD	t-value	Estimate	SD	t-value
Intercept	9.641	0.041	233.75***	8.523	0.070	121.40***
Dispersal	-0.429	0.337	-1.27	1.194	0.530	2.25*
Stressor flux	0.104	0.413	0.252	-0.310	0.715	-0.43
Time	0.011	0.009	1.20	0.061	0.010	6.33***
Time ²	0.001	0.001	1.90	-0.003	0.001	-4.97***
dispersal x stressor flux	-4.43	3.34	-1.33	8.783	5.345	1.64
Dispersal x time	0.093	0.074	1.26	0.346	0.073	4.73***
Dispersal x time ²	-0.012	0.004	-2.82**	-0.009	0.005	-1.84
Stressor flux x time ²				0.018	0.003	6.17***
Stressor flux x time	-0.050	0.043	-1.15			
Dispersal x stressor flux x time	1.210	0.353	3.43***			
Dispersal x stressor flux x time ²				-0.082	0.023	-3.61***

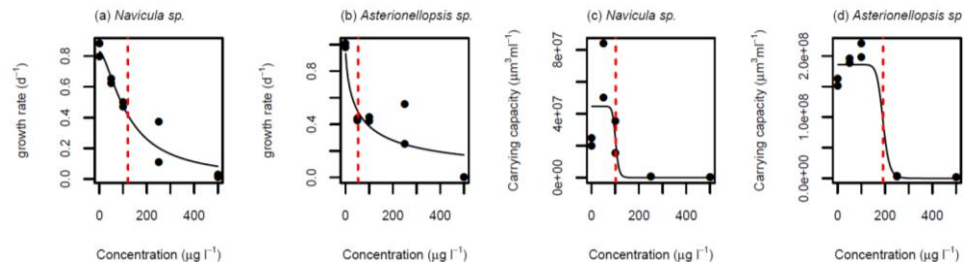


Fig. 4.6. The growth rate of (a) *Navicula* sp. and (b) *Asterionellopsis* sp. and the carrying capacity of (c) *Navicula* sp. and (d) *Asterionellopsis* sp. as function of the stressor (atrazine) concentration. The dots represent the data, the curve represents the fitted logistic dose-response relationship (Eq. 4.4). The dotted line represents the EC_{50} i.e. concentration at which the growth rate and carrying capacity are reduced with 50%.

4.4 Discussion

The obtained results empirically demonstrate that stressor fluxes can change the relationship between beta-diversity and regional productivity and offer insight into the underlying mechanisms. In our study system, this change was the result of dispersal affecting regional and local productivity differently in the presence of the stressor flux, compared to when no flux was present. In contrast, we did not find the stressor flux to alter dispersal effects on beta-diversity as these were negative across all stressor flux levels.

4.4.1 The relationship between beta-diversity and regional productivity in the absence of the stressor flux.

In the absence of the stressor flux, we predicted a positive relationship between beta-diversity and regional productivity, because dispersal would decrease both beta-diversity and regional productivity. Dispersal was expected to reduce regional productivity by disrupting local dynamics when exporting well-adapted (and therefore highly productive) organisms while importing less well-adapted, and thus less-productive, organisms (Mouquet and Loreau 2003). Contrary to this expectation, we found only found a positive relationship between beta-diversity and regional productivity on day 24 only, while the relationship was weak or absent before (Fig. 4.3). At first, this seems surprising because dispersal disrupted local dynamics in the unstressed community by moving organisms of *Asterionellopsis* sp. and *Navicula* sp. from the unstressed to the stressed community. This movement was due to higher density in the unstressed than in the stressed community in absence of dispersal, which reflects the negative effects of the chemical stressor on growth. Although a reduction of the density of the best-adapted strains in the unstressed community is expected to decrease productivity, dispersal did not induce a regional productivity decrease, except on day 24. A main reason for this is that the negative effect of dispersal in the unstressed community (essentially, the withdrawal of biomass) was compensated by a positive effect of dispersal in the stressed community. Moreover, negative dispersal effects on the productivity of the unstressed community were often low. Indeed, dispersal-induced productivity decreases are generally found at dispersal rates that are high compared to the reproduction rate (40%-100%) (Leibold et al. 2017). In the present study, the highest dispersal rate was approximately only 5% of the exponential growth rate of *Asterionellopsis* sp. without the stressor.

Only on day 24, we found a positive relationship between beta-diversity and regional productivity (Fig. 4.3). On day 24, dispersal reduced regional productivity by reducing the productivity of the unstressed community (Fig. 4.4). It is not clear why dispersal reduced the productivity in the unstressed community only on day 24 and not on earlier days. Moreover, the negative effect of dispersal on productivity in the unstressed community was unexpectedly high (80%), given that the highest dispersal rate was only 20%. A part of the negative effect of dispersal on productivity was probably due the dispersal-induced removal of organisms of *Navicula* sp. from the unstressed community on day 20, limiting biovolume production between day 20 and 24. However, the reduction in productivity was also the result of cell lysis in the communities at a high dispersal rate. Cell lysis may occur when nutrients are limited, or waste products are accumulating (Brussaard et al. 1997, Brussaard and Riegman 1998, Andersen and Kawachi 2005). However, it is not clear why cell lysis occurred first in the

highest dispersal treatments. A possible explanation is that dispersal altered interactions between algae strains or interactions between algae and other organisms such as bacteria, which are shown to influence algae growth through facilitation or competition (Cole 1982, Grossart 1999). Our results thus indicate that an increasing homogenization through dispersal can reduce regional productivity in the absence of a stressor flux, as was found before in other marine micro-algae communities (Eggers et al. 2012, de Boer et al. 2014). However, this reduction may be caused by more complex interactions than predicted by theory in Mouquet and Loreau (2003).

In absence of the stressor flux, dispersal increased the productivity of the stressed community, but this effect was initially too weak to increase regional productivity because the high stressor concentration disabled the growth of the introduced organisms (Fig. 4.6).

4.4.2 The relationship between beta-diversity and regional productivity in the presence of the stressor flux.

In the presence of the stressor flux, we predicted a negative relationship between beta-diversity and regional productivity because dispersal would decrease beta-diversity but increase regional productivity. Theory predicts that under changing environmental conditions dispersal can increase productivity by introducing strains that are better adapted (Loreau et al. 2003a). As predicted, we found negative relationships between beta-diversity and regional productivity in the presence of the stressor flux from day 12 (Fig. 4.3). Dispersal increased regional productivity by increasing the productivity of the stressed community, while not affecting the productivity of the unstressed community (Fig. 4.5).

The stressor flux reduced the stressor concentration in the stressed community, generating recovery by increasing the growth rate of the stress-tolerant strains (Fig. 4.6). Instead of introducing new strains to the stressed community, dispersal introduced the strains that were also most abundant in the stressed community without dispersal because the most stress-tolerant strains, *Asterionellopsis* sp. and *Navicula* sp. dominated the unstressed as well as stressed community. By introducing organisms of *Asterionellopsis* sp. and *Navicula* sp., dispersal increased recovery in the presence of the stressor flux (Fig. 4.5). The positive effect of dispersal on the productivity of the stressed community was stronger in the presence than in the absence of the stressor flux, because the dispersed organisms could grow in the presence of the stressor flux while their growth was suppressed in the absence of the stressor flux because of the high stressor concentration (Fig. 4.6).

The fact that dispersal can reinforce recovery by subsidizing population growth was also demonstrated in communities that were exposed to heat stress by de Boer et al. (2014). However, in de Boer et al. (2014), the stressor was applied synchronically across all

communities, while the environmental conditions in our study were spatiotemporally varied. There are some studies that applied temporal fluctuations (Steiner et al. 2011, Guelzow et al. 2014), but they only alternated the environment between two conditions. Such rapid transitions select for the strains that persist in the extreme conditions. Instead, in the present study, the stressor flux gradually changed the stressor concentration, allowing the community composition to track this change. As such, negative relationships between beta-diversity and regional productivity initially appeared at the highest stressor flux level and only later at the low- and medium stressor flux level.

In the unstressed community, the stressor flux increased the concentration of the chemical stressor. However, dispersal did not affect productivity in the unstressed community by introducing stress-tolerant strains, because the strain which was most stress-tolerant, *Asterionellopsis* sp., dominated the unstressed community early in the experiment (Fig. 4.4). Because the stressor effect on the carrying capacity of *Asterionellopsis* sp. was nonlinear (Fig. 5d), the effect of the increasing stressor concentration on productivity was small in the unstressed community. When the concentration proceeded from the initial to the final concentration in the unstressed community ($86 \mu\text{g l}^{-1}$ for the highest stressor flux), the decrease of the carrying capacity of *Asterionellopsis* sp. in the unstressed community was therefore almost negligible.

The stressor flux generated a negative spatial covariance of the stressor concentration between the unstressed and stressed community, homogenizing the environmental conditions and decreasing the difference in productivity between the unstressed and stressed community. Hence, the effect of dispersal on beta-diversity and regional productivity decreased at the end of the experiment, which resulted in the absence of a significant relationship between beta-diversity and regional productivity on day 24 at the highest stressor flux level. Stressor fluxes may thus reduce dispersal effects on diversity and productivity in the long term.

4.4.3 Concluding remarks

Our study system and design are characterized by five aspects that should be borne in mind when extrapolating to other systems or scenarios. First, competitive interactions were strong, which induced the dominance of two algae strains. Planktonic microalgae systems are often subject to strong interspecific competition because of the limited spatial heterogeneity (Giller et al. 2004), and are hence in laboratory conditions generally dominated by only a few species (Mensens et al. 2015, Baert et al. 2016a, 2017). Second, in the present study, the unstressed and stressed community were dominated by the same algae strains. However, how

community compositions change highly depends on the correlation between competitive abilities and the sensitivity to the stressor (De Laender et al. 2016, Baert et al. 2017, Spaak et al. 2017). Third, all species from the regional species pool were initially present in each community, and we did not perform dispersal of species that were not initially present in the local communities (Lessard et al. 2012). Dispersal of new species could have introduced more stress-tolerant or more competitively dominant species, leading to a stronger positive effect of dispersal on productivity. Fourth, in this study, the stressor flux was manipulated by pipetting, while stressor fluxes are often caused by agents such as water currents and diffusion. The way the stressor flux was manipulated, is comparable to a homogenization of the chemical stressor, in which the concentration gradient and thus the rate of homogenization decreases over time. This is a simplification of natural systems, where the concentration of chemical stressors also decreases over time through other mechanisms such as the degradation of chemical stressors or the accumulation of chemical stressors in the sediment. Last, dispersal were enforced by moving organisms between the patches. When organisms move passively, stressor fluxes and dispersal are often linked. Our results indicate that in such cases, regional productivity can be positively affected by dispersal. When organisms move actively, avoidance of less appropriate patches can occur, e.g. because of the presence of a chemical stressor (Araújo et al. 2016), or because of a lower nutrient availability (Byers 2000, Kennedy and Ward 2003). Such avoidance behavior precludes positive dispersal effects under stressor fluxes. In the present study, we also applied symmetric dispersal (dispersal probability in both directions is equal) and equal per capita dispersal rates, which have been shown to favor competitive dominant species (Salomon et al. 2010). Many habitats are characterized by asymmetric dispersal, e.g. planktonic organisms follow the water current, and plant seeds disperse according to the wind direction. Moreover, organisms show different per capita dispersal rates (Edelaar and Bolnick 2012, Bonte and Dahirel 2017). Therefore, our study is only a first step to understand beta-diversity – productivity relationships and studies that use other dispersal mechanisms and properties are required.

Previous studies have shown that the relationship between beta-diversity and productivity is often positive (Chase and Leibold 2002, Chalcraft et al. 2004, Chase and Ryberg 2004, Harrison et al. 2006). While this study found a positive relationship in the absence of the stressor flux, this relationship shifted to negative in the presence of the stressor flux. Dispersal and a stressor flux may thus interact in regulating the relationship between beta-diversity and productivity. This interaction can have consequences when managing ecosystem functioning of landscapes in which some local communities are exposed to growth-affecting agents, such as the chemical stressors that were used in this study. The concentration at which we applied atrazine can usually only be found in agricultural areas after application (Graymore et al.

2001). Although background concentrations are generally much lower (Nödler et al. 2013), chemical stressors are abundant in many marine waters (Halpern et al. 2008, Abessa et al. 2018) and the present experiment helps to gain mechanistic insight how the flux of chemical stressors may affect the relationship between diversity and productivity. Based on our study, we recommend further investigating how these fluxes affect communities and interact with the dispersal of organisms.

5

The effect of pesticide stress on the diversity and productivity of micro-algae communities along a connectivity gradient

Redrafted from: De Raedt J., Janssen C.R., Baert J.M., De Laender F. 2019. The effect of pesticide stress on the diversity and productivity of marine micro-algae communities along a connectivity gradient. *To be submitted*.

Abstract

Landscapes are composed of communities that are connected through dispersal, i.e. the movement of organisms. We investigated how a chemical stressor and connectivity change the productivity and diversity in landscapes using a microcosm experiment. Landscapes contained eight patches of marine micro-algae communities. In the control landscapes, all communities were unexposed, while in the landscapes with chemical application, half of the communities were exposed to the herbicide atrazine ($100 \mu\text{g/l}$). Within each treatment, we created a connectivity gradient by varying the number of connections among communities. Connectivity did not affect the productivity or diversity of the communities in the control landscapes. In the landscapes with chemical application, connectivity did not affect regional productivity as connectivity increased the productivity of the exposed patches, but at the same time decreased the productivity of the unexposed patches to a similar extent. Within the landscapes with chemical application, connectivity increased regional diversity because connectivity increased the relative density of the stress-tolerant species on a landscape scale. Moreover, connectivity increased the diversity of the unexposed patches because the stress-tolerant species was moved from the exposed patches, where it could persist, to the unexposed patches, where it was almost outcompeted. In contrast, connectivity decreased the diversity of the exposed patches because the relative density of the stress-sensitive species, which was dispersed from the unexposed to the exposed patches, exceeded the relative density of the stress-tolerant species. This study shows that connectivity has strong effects on how environmental stressors like chemicals have an impact on biodiversity and ecosystem functions.

5.1 Introduction

Studies have shown that chemical stressors, such as metals and pesticides, can alter the productivity and diversity of communities (Mcmahon et al. 2012, Halstead et al. 2014, Viaene et al. 2015, Baert et al. 2016a, De Laender et al. 2016). Although these studies were commonly performed in isolated communities, landscapes are in reality composed of multiple local communities that are interconnected through dispersal, i.e. the movement of organisms (Leibold et al. 2004, Bonte and Doherty 2017). Such landscapes often contain both exposed and unexposed patches because chemical emission and fate can create spatially heterogeneous distribution patterns of chemicals (Weigel et al. 2002, Waeles et al. 2009, Deschutter et al. 2017).

The effect of connectivity in landscapes where chemicals are heterogeneously distributed has mainly been studied at the population-level (Spromberg et al. 1998, Van den Brink et al. 2007, Brock et al. 2010). For instance, the Mastep model (Metapopulation model for Assessing Spatial and Temporal Effects of Pesticides) is a well-known tool to investigate how chemical exposure affects interconnected populations (Galic et al. 2012a, Focks et al. 2014). When chemical exposure decreases the productivity of the exposed patches, dispersal from unexposed patches may compensate for this productivity loss (Spromberg et al. 1998, Schriever et al. 2007, Brock et al. 2010). This positive effect of dispersal on the productivity of the populations in the exposed patches can create a negative effect on productivity in the unexposed patches (Spromberg et al. 1998, Van den Brink et al. 2007, Brock et al. 2010).

When communities instead of populations are connected in a heterogeneous environment, patches may not only differ in productivity but also in composition. Such differences in composition are the result of trade-offs in competitive strength and stress tolerance which induces the replacement of stress-sensitive by stress-tolerant species (Mcmahon et al. 2012, Baert et al. 2016a, De Laender et al. 2016, Spaak et al. 2017). Dispersal can affect these compositional shifts. Dispersal can introduce species that have a higher performance than the resident species, increasing regional productivity (Loreau et al. 2003a, Symons and Arnott 2013, de Boer et al. 2014, De Raedt et al. 2016). Such effect is also referred to as the spatial insurance effect (Loreau et al. 2003a). However, when dispersal disrupts local dynamics, it may likewise reduce regional productivity (Mouquet and Loreau 2003, de Boer et al. 2014, Leibold et al. 2017). Dispersal disrupts local dynamics when it removes resident organisms that perform well under the local environmental conditions and replaces them by organisms that perform less well under the local environmental conditions (Mouquet and Loreau 2003). However, experimental evidence for a negative dispersal effect on regional productivity is

scarce (Leibold et al. 2017) because negative dispersal effects often only occur at a very high dispersal rate (Howeth and Leibold 2010a, Lindström and Östman 2011).

Regional diversity is often higher in heterogeneous than in homogeneous landscapes because more species can find an appropriate patch where they perform well (Tilman 1994, Amarasekare 2003). Dispersal is demonstrated to decrease regional diversity in such landscapes by creating regional dominants that exclude other species, as such homogenizing community composition across the landscape (Mouquet and Loreau 2003, Matthiessen et al. 2010a). Dispersal-local diversity relationships are predicted to have a unimodal shape (Mouquet and Loreau 2003). At low dispersal rates, dispersal increases local diversity by moving species from patches where they are abundant to patches where they are less abundant or even absent. At high dispersal rates, dispersal reduces local diversity as competitive subdominant species are regionally excluded (Mouquet and Loreau 2003, Matthiessen et al. 2010a, Eggers et al. 2012).

Most studies that investigate the effect of dispersal in heterogeneous landscapes only contain two or three patches (e.g. Matthiessen et al. 2010a, Pedruski and Arnott 2011, Eggers et al. 2012, Limberger et al. 2014, Souffreau et al. 2014). However, real landscapes are spatially extended and contain multiple patches (Davies et al. 2009, Carrara et al. 2012, 2014, Seymour and Altermatt 2014). Within spatially-extended landscapes, community composition depends on the position of the patch in the network, which is not the case for simple two-patch communities (Carrara et al. 2012, Seymour and Altermatt 2014).

Until now, the few studies that investigated spatially extended landscapes only used a few connectivity levels (Davies et al. 2009, Carrara et al. 2012, 2014). Moreover, they created a heterogeneous environment by spatially varying resources (Davies et al. 2009) or by applying random disturbances in some patches of the landscape (Altermatt et al. 2011b, Carrara et al. 2012). Varying resources often generates opposite effects on species, increasing the growth of some species, while decreasing the growth of others. However, such variations do not necessarily change productivity. In contrast, the application of an environmental stressor affects the per-capita growth rate of all species negatively, decreasing the productivity of the exposed patches (but see Spaak et al. 2017) and therefore regional productivity. Also random disturbances decrease the productivity of the affected patches (Matthiessen et al. 2010b, Altermatt et al. 2011b). However, those random disturbances affect all species equally by removing a fixed proportion of each species. In contrast, environmental stressors such as chemicals have species-specific effects, affecting some species more than others (De Laender et al. 2016, Baert et al. 2017). Therefore, there is a need for studies that address

how connectivity affects the diversity and productivity in spatially extended landscapes exposed to environmental stressors.

To investigate the combined effect of environmental stress and connectivity, we conducted a microcosm experiment with communities of marine micro-algae. We constructed landscapes of 8 interconnected communities (patches) and manipulated the application of a chemical and connectivity using a crossed design (Fig. 5.1). The chemical application treatment contained two levels; in the landscapes with atrazine application, half of the patches was exposed to the herbicide atrazine; in the control landscapes none of the patches was exposed. We defined connectivity as the number of connections between the patches of a landscape and manipulated connectivity by creating landscapes with a different number of connections. We selected two algae strains that exhibited a trade-off between competitive ability and toxicant sensitivity. *Odontella* sp. (OD) was the strongest competitor, while *Dactyliosolen* sp. (DACT) was most tolerant to atrazine.

Positive effects of dispersal on regional productivity are only expected to occur when new species are introduced to patches (Loreau et al. 2003a). Moreover, there are hardly any experiments that find a negative effect of dispersal on regional productivity (Leibold et al. 2017). In our system, all species were initially present in all patches. Therefore, we hypothesized that connectivity would not affect regional productivity in the control landscapes or the landscapes with chemical application (H1). At a local scale, we expected that connectivity would increase the redistribution of organisms in the landscapes with chemical application (e.g. Spromberg et al. 1998). Therefore, we hypothesized that connectivity would increase the productivity of the exposed patches, while decreasing the productivity of the unexposed patches (H2).

In the patches that were exposed to atrazine, we expected that the tolerant species DACT would replace the toxicant-sensitive, but regionally dominant, species (OD). We therefore hypothesized that chemical application would increase regional diversity but that connectivity would decrease regional diversity in the landscapes with chemical application by increasing the regional density of the regional dominant species OD (H3). At a local scale we expected to find a hump-shaped relationship between connectivity and diversity in the landscapes with chemical application (Mouquet and Loreau 2003) (H4). At low connectivity, connectivity would increase the relative density of DACT in the unexposed patches and increase the relative density of OD in the exposed communities, acting to increase local diversity. At high connectivity, connectivity would increase the relative density of the regional dominant species, acting to decrease local diversity.

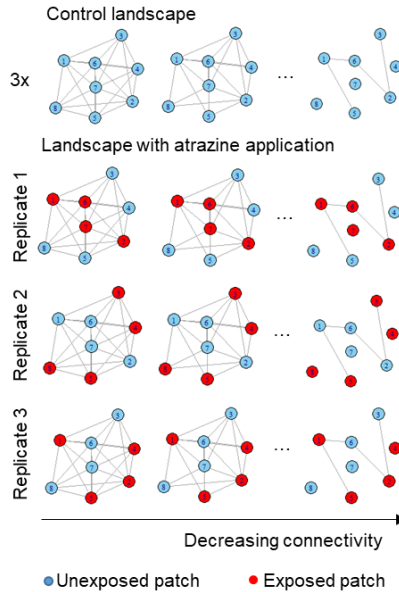


Fig. 5.1: We used a crossed design of chemical application and connectivity. The chemical application treatment contained 2 levels: control landscapes (none of the patches was exposed), and the landscapes with chemical application (4 of the 8 patches were exposed). The connectivity treatment contained 6 levels. All treatments were replicated three times.

To test these hypotheses, we determined the effect of chemical application and connectivity on regional and local productivity and diversity after 12 and 30 days. To explain how atrazine application and connectivity affected diversity, we also investigated the effect of both factors on the relative density of the chemical-tolerant species. Last, we examined if connectivity changed the chemical concentration in the communities and if a change of the chemical concentration affected productivity. To this end, we measured the effect of atrazine on the biovolume of the algae in competition under isolated conditions.

5.2 Materials and methods

5.2.1 Study system and overall design

We used two strains of marine micro-algae of the class *Bacillariophyceae* (diatoms), which were collected in the Belgian part of the North sea during spring 2017. The algae were isolated using the protocol of Andersen (2005) and grown in f/2 medium based on instant ocean artificial seawater. All cells of a strain thus originated from the same initial algae cell. The strains were selected based on preliminary experiments, where we found a trade-off between competitive ability and toxicant sensitivity. *Odontella* sp. (OD) was the strongest competitor, while *Dactyliosolen* sp. (DACT) was most tolerant to atrazine (Appendix D Table D1, Fig. D1,

D2). Algae were grown in Erlenmeyer flasks in a climate room at $20 \pm 1^\circ\text{C}$ with $35 \mu\text{mol m}^{-2}$ light intensity. We used a full factorial design containing two atrazine application treatments (1 without and 1 with atrazine application) and 6 connectivity levels. Each treatment was replicated three times. In total, our experiment thus contained 36 landscapes: two chemical application treatments, six connectivity levels and three replicates. At the start of the experiment, algae were added to each community at a total initial density of $0.225 \text{ mm}^3 \text{ l}^{-1}$ per strain. The experiment was started during two consecutive days. Three connectivity levels per exposure treatment and replicate were established on day 1, while the other three were established on day 2. We established the experiment on two consecutive days because the experimental set-up was too large to manipulate dispersal in all landscapes on the same day.

5.2.2 Experimental treatments

The atrazine application treatment contained two levels: in the control landscapes, none of the patches were exposed to atrazine; in the landscapes with atrazine application, four of eight communities were exposed to the photo-inhibiting chemical atrazine at a concentration of $100 \mu\text{g l}^{-1}$. Per landscape, we distinguished two types of patches: unexposed and exposed patches. The unexposed patches were unexposed in both the control landscapes and the landscapes with atrazine application. The exposed patches were unexposed in the control landscapes but exposed in the landscapes with atrazine application. Among the replicates of the exposed treatment, we varied the location of the exposed patches in the landscape. Atrazine was added in the most-connected patches in the first replicate, in the least-connected patches for the second replicate and in the averagely-connected patches for the third replicate. In replicate 1 for instance, patches 1, 2, 6 and 7 were the most-connected patches and were therefore exposed to atrazine. In contrast, patches 3, 4, 5 and 8 were the least-connected patches and were therefore not exposed to atrazine. (Appendix D Table D2).

We applied six connectivity levels. Each connectivity level had four connections less than the previous connectivity level. The highest connectivity corresponded to 24 connections, while the lowest connectivity only had 4 connections (Fig. 5.1). At the five highest connectivity levels, all communities were still connected. At the lowest connectivity level, 3 out of 8 communities were isolated (Fig 5.1).

Dispersal between communities was performed by exchanging 1 ml (3.33%) of medium per connection in each direction. Therefore, organisms in a more-connected patch had a higher dispersal probability than in a less-connected patch. Moreover, dispersal was symmetrical as the proportion of organisms that was exchanged in each direction was equal. To minimize the transfer of medium among communities, algae cells and medium were separated using centrifugation. To do so, 10 mL was removed from the culture and placed in a glass centrifuge

tube. Next, this tube was centrifuged at 800 rpm (acceleration 5 m/s^2 , deceleration 3 m/s^2) during 20 minutes. 8 ml of supernatant was removed and stored for toxicant and nutrient analysis. Next, 200 μl of the precipitate was added to each culture that was connected to the source culture. The remaining precipitate was added to the source culture together with 9 ml of clean medium. By using this method, the amount of culture that was centrifuged was equal among all communities and treatments. Moreover, new medium was added to keep the toxicant concentration stable (atrazine is degraded by light) and to delay nutrient depletion.

Next to the connectivity experiment, we also grew the algae in an isolated competition experiment (no connections). We applied five atrazine concentrations (0, 25, 50, 100 and 200 $\mu\text{g l}^{-1}$). We added the algae to f/2 medium at a total initial density of $0.225 \text{ mm}^3 \text{ l}^{-1}$ per strain. Algae were placed together with the flasks of the connectivity experiment to have identical growth conditions. As in the landscape experiment, 30% of the medium was renewed every 3 days. To do so, 10 mL was removed from the culture and placed in a glass centrifuge tube. This tube was centrifuged at 800 rpm (acceleration 5 ms^{-2} , deceleration 3 ms^{-2}) during 20 minutes. 8 ml of supernatant was removed and stored for toxicant and nutrient analysis. Last, the precipitate was moved back into the culture together with 9 ml of new medium.

5.2.3 Measurements and analyses

1 ml samples were taken for cell counting before connectivity was manipulated. Samples were inoculated with 200 μl lugol and stored at 4°C . Cell counting was performed by using an inverted microscope with a whipple grid in the ocular. During the manipulation of connectivity, we also collected samples for atrazine analysis. Atrazine samples were stored at -20°C in glass tubes and analyzed using mass chromatography, coupled with a mass spectrometer (Appendix D Table D3).

Local productivity was obtained by transforming the cell counts to biovolumes based on the cell-specific biovolume (Hillebrand et al. 1999). Regional productivity was obtained by calculating the sum of the biovolume of all patches within a landscape. Because of the variability in cell sizes among strains, diversity was determined according to individual strains' biomass calculated as biovolume (Hillebrand et al. 1999). Biodiversity was measured using the Shannon diversity index H_j in patch j (Eq. 5.1), using the vegan package (Oksanen et al. 2014) in R and was calculated as:

$$H_j = - \sum_{i=1}^n p_{i,j} \ln p_{i,j} \quad (\text{Eq. 5.1})$$

where $p_{i,j} = m_{i,j} / \sum_{i=1}^n m_{i,j}$ with $m_{i,j}$ the biovolume of species i in patch j and n the number of species (2). To measure local diversity, the Shannon index was calculated per patch. To measure regional diversity, the Shannon index was calculated across the entire landscape.

5.2.4 Statistical analyses

The statistical analyses for productivity, diversity and the transformed relative density of the stress-tolerant species were performed for days 12 and 30 separately using mixed linear effect models. For the first analysis, the log transformed regional productivity was the response variable and atrazine application, connectivity, their interaction, and start day were the predictor variables (Eq. 5.2).

$$\begin{aligned}
 \text{regional productivity}_{ij} &= \alpha + \beta_1 * \text{atrazine application}_j + \beta_2 * \text{connectivity}_{ij} + \beta_3 \\
 &* \text{start day}_{ij} + \beta_4 * \text{atrazine application}_j * \text{connectivity}_{ij} \\
 &+ \varepsilon_{ij}
 \end{aligned} \tag{Eq. 5.2}$$

With $\text{regional productivity}_{ij}$ regional productivity for the i th observation within the atrazine application treatment j . α is the estimated intercept and β_1, \dots, β_4 are the estimated slopes of the linear model. ε_{ij} are the residuals, with $\varepsilon_{ij} \sim N(0, \sigma_j^2)$. σ_j^2 is the estimated variance per atrazine application treatment. We did not add a variance structure for connectivity as this did not increase model performance (based on ANOVA for nested models). A similar analysis was performed for regional diversity and the regional log transformed relative abundance of (DACT+1)

Next, we analyzed the effect of atrazine application, exposure and connectivity on the local productivity on days 12 and 30 separately. We used the log transformed local productivity as response variable and used atrazine application, exposure (unexposed versus exposed patch), connectivity, their interactions and start day as predictor variables using Eq. 5.3.

$$\begin{aligned}
 \text{local productivity}_{ijk} &= \alpha + \beta_1 * \text{atrazine application}_j + \beta_2 * \text{exposure}_k + \beta_3 \\
 &* \text{connectivity}_{ijk} + \beta_4 * \text{start day}_{ijk} + \beta_5 \\
 &* \text{atrazine application}_j * \text{exposure}_k + \beta_6 \\
 &* \text{atrazine application}_j * \text{connectivity}_{ijk} + \beta_7 * \text{exposure}_k \\
 &* \text{connectivity}_{ijk} + \beta_8 * \text{atrazine application}_j * \text{exposure}_k \\
 &* \text{connectivity}_{ijk} + \varepsilon_{ijk}
 \end{aligned} \tag{Eq. 5.3}$$

$local\ productivity_{ijk}$ is the local productivity of the the i th observation with atrazine application j and exposure k . α is the estimated intercept and β_1, \dots, β_8 are the estimated slopes of the linear regression. The residuals ε_{ijk} are given by

$$var(\varepsilon_{ijk}) = \sigma_j^2 \times \sigma_k^2 \times (\delta_{1jk} + |connectivity_{ijk}|^{\delta_{2jk}})^2 \quad (\text{Eq. 5.4})$$

to correct for heteroscedasticity. With σ_j^2 and σ_k^2 the variance per atrazine application treatment and exposure level respectively. δ_{1jk} and δ_{2jk} the estimated parameters of the power variance structure. Note that those parameters depend on the atrazine application treatment and exposure level. Furthermore, we corrected for spatial correlation. As such:

$$cor(\varepsilon_{ijk}, \varepsilon_{ljk}) = \begin{cases} 1 & \text{if } i = l \\ h(\varepsilon_{ijk}, \varepsilon_{ljk}, \rho) & \text{else} \end{cases} \quad (\text{Eq. 5.5})$$

We tested if the addition of the different terms of the variance structure (i.e. σ_k^2 , σ_l^2 and $(\delta_{1kl} + |connectivity_{ijk}|^{\delta_{2kl}})^2$) significantly increased model performance using the ANOVA test for nested models in R (R. Core Team 2016) and by plotting the model residuals as a function of the predictor variables and the predicted values as suggested by Zuur et al. (2009). A term that did not increase model performance was not included in the analysis.

We repeated the same analyses for diversity and the local log transformed relative density of DACT+1 (to avoid any infinite values when taking a logarithm). When analyzing local diversity, we initially included connectivity as a first- and second order predictor to test possible hump-shaped effects. If the addition of the second-order term did not give a better model performance according to the ANOVA test, we removed connectivity as a second-order predictor.

Although the algae and medium were separated using centrifugation, this separation was not perfect and we hence expected to find a small but potentially important effect of connectivity on the atrazine concentration. Therefore, we performed a separate analysis to investigate if the effect of connectivity on local biovolume was caused by a change of the atrazine concentration rather than by the dispersal of the algae. Therefore, we investigated which factors significantly affected the measured productivity $productivity_{measured,i}$ by using a generalized non-linear model (Eq. 5.5).

$$\begin{aligned}
& (\log_{10}(\text{productivity}_{\text{measured},i})) \\
& = (\log_{10}(\text{productivity}_{\text{calculated},i})) \\
& + \text{treatment}_i(\text{unexposed} = \text{true}) * \alpha * \text{local con}_i \\
& + \text{treatment}_i(\text{exposed} = \text{true}) * \frac{\beta * \text{local con}_i}{\text{local con}_i + \gamma} + \varepsilon_i
\end{aligned} \tag{Eq. 5.6}$$

With α, β, γ the values of the regression coefficients and ε_i the normally distributed residuals. $\text{productivity}_{\text{calculated},i}$ is the biovolume of each patch i within a landscape that was calculated by using the measured concentration of atrazine conc within each patch. This calculation thus returns the expected biovolume should dynamics only be influenced by the (unintended) movement of atrazine, ignoring the effect of algae dispersal on productivity. $\text{productivity}_{\text{calculated},i}(\text{conc})$ is calculated as follows:

$$\begin{aligned}
& \text{productivity}_{\text{calculated},i}(\text{conc}) \\
& = c + \frac{d - c}{1 + \exp(b * (\log(\text{conc}) - \log(EC_{50})))}
\end{aligned} \tag{Eq. 5.7}$$

b, c, d and EC_{50} are the estimated parameters of the four-parametric log-logistic function. EC_{50} represents the inflection point, i.e. the concentration at which the productivity is reduced by 50%. The parameters were determined using the data from the isolated competition experiment. Parameters were derived by fitting the four-parametric log-logistic function to total productivity on day 30 day by using the *drc* function in R.

In Eq. 5.6, local con_i is the local connectivity (the number of the incident connections) of a patch i . Local connectivity instead of regional-scale connectivity was used as a predictor variable because it is a patch-dependent attribute, while regional connectivity is a landscape-dependent attribute. Moreover, when $\text{local con} = 0 \Rightarrow \log_{10}(\text{productivity}_{\text{measured},i}) = \log_{10}(\text{productivity}_{\text{calculated},i}) + \varepsilon_i$

If $\text{productivity}_{\text{measured},i}$ was affected by the dispersal of algae, local connectivity would be a significant predictor of $\text{productivity}_{\text{measured},i}$. Atrazine was only measured for samples of replicate 1. We hence only performed statistical analyses using the local productivity of patches 1, 2, 6 and 7 of replicate 1. These analyses were performed for each patch separately to avoid spatial correlation. The p-values were corrected using the Bonferroni post hoc test. We used a non-linear (saturating) model as this resulted in a better model fit than when using a linear model (based on residual plot and local connectivity – local productivity plots (Appendix D Fig. D5, D6, D8, D9)). To fit this non-linear model, we used the *nls* function in R (R. Core Team 2016).

5.3 Results

Atrazine application in the landscape changed productivity and diversity at the regional and local scale. Moreover, while connectivity did not affect the control landscapes, it did change the productivity and diversity of the landscapes where atrazine was applied.

5.3.1 Productivity

Atrazine application on a landscape level reduced regional productivity during the entire experiment (Table 5.1, Fig. 5.2 a, d). On day 12, atrazine application also changed the effect of connectivity on regional productivity. Connectivity did not affect the regional productivity of the control landscapes, while it increased the regional productivity in the landscapes with atrazine application (Table 5.1, Fig. 5.2 d). On day 30, atrazine did not change the effect of connectivity on regional productivity as connectivity did not affect regional productivity in the control landscapes or in the landscapes with atrazine application (Table 5.1, Fig. 5.2 d).

On day 12, atrazine application on a landscape level did not affect the productivity in the unexposed patches but decreased the productivity in the exposed patches (Table 5.2, Fig. 5.2 b, c). We found a significant interaction effect between atrazine application, connectivity and patch exposure. Therefore, connectivity increased the productivity in the exposed patches in the landscapes with atrazine application, as was also seen at a regional scale (Fig. 5.2 a, c).

On day 30, atrazine application did not affect the productivity in the unexposed patches but decreased the productivity in the exposed patches (Table 5.2, Fig. 5.2 e, f). We found a significant interaction effects between atrazine application and connectivity, showing that connectivity decreased the productivity of the unexposed patches within the landscapes with atrazine application. Moreover, a significant interaction effect between atrazine application, connectivity and patch exposure demonstrates that connectivity increased the productivity of the exposed patches (Fig. 5.2 e, f).

Measuring the chemical concentration showed that connectivity slightly reduced the chemical concentration in the exposed patches (Appendix D Table D7, Fig. D3). Therefore, we predicted the total productivity at the measured concentrations by using the dose-response relationship of the competition experiment (Appendix D Fig. D4). For the exposed communities, the predicted productivity were consistently lower than those measured in the experiment (Fig. 5.3, triangles).

Table 5.1. Results of the linear model with atrazine application, connectivity, their interaction and start day as predictor variables and the log transformed regional productivity as response variable. Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Day 12			Day 30		
	Value	SD	t-value	Value	SD	t-value
Intercept	10.252	0.019	544.88***	10.600	0.012	865.07***
Start day	0.105	0.014	7.54***	-0.005	0.011	-0.43
Atrazine app	-0.302	0.032	-9.39***	-0.317	0.040	-7.94***
Connectivity	0.000	0.001	0.27	-0.005	0.001	-0.59
Atrazine app x Connectivity	0.006	0.002	3.04**	0.001	0.003	0.21

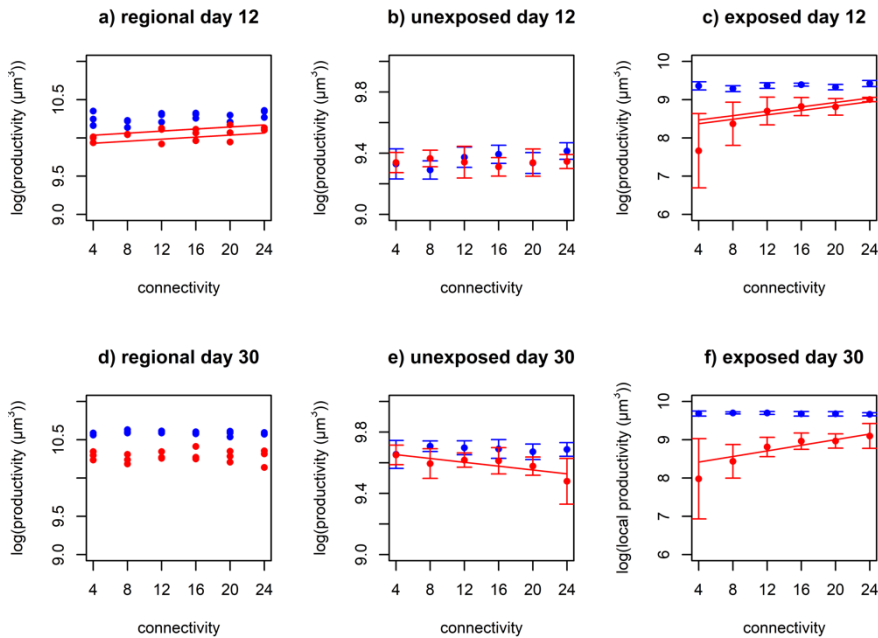


Fig. 5.2. The log transformed productivity in function of connectivity on days 12 and 30. Panels a and d represent the effect of connectivity on regional productivity (3 replicates) in the control landscapes (blue) and the landscapes with atrazine application (red). Panels b and e represent the effect of connectivity on the local productivity of the unexposed patches in the control landscape (blue) and the landscapes with atrazine application (red) (mean \pm SD). Panels c and f represent the effect of connectivity on local productivity of the exposed patches in the control landscape (blue) and the landscapes with atrazine application (red) (mean \pm SD). The regression lines are only shown in case of a significant effect when using a mixed linear effect model (Table 5.1, Table 5.2).

Table 5.2. Results of the generalized linear model with connectivity, atrazine application (on a landscape level), patch exposure, their interactions and start day as predictor variables and the log transformed mean local productivity on days 12 and 30 as response variable. Significance levels: * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

	Day 12			Day 30		
	Value	SD	t-value	Value	SD	t-value
Intercept	9.299	0.018	510.89***	9.690	0.021	466.37***
Start day	0.095	0.012	7.65***	-0.007	0.013	-0.58
Atrazine app.	-0.021	0.029	-0.71	-0.011	0.036	-0.31
Patch exposure	0.016	0.022	0.743	0.012	0.021	0.58
Connectivity	0.001	0.001	0.66	0.000	0.001	0.04
Atrazine app x patch exposure	-1.036	0.135	-7.65***	-1.420	0.136	-10.45***
Atrazine app x connectivity	0.000	0.002	0.08	-0.006	0.002	-2.69**
Patch exposure x connectivity	-0.001	0.001	-0.71	-0.001	0.001	-0.84
Atrazine app x patch exposure x connectivity	0.028	0.007	4.41***	0.044	0.007	5.99***

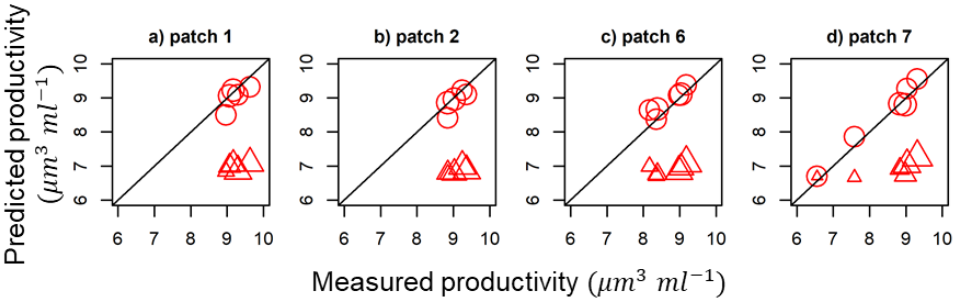


Fig. 5.3. Predicted vs. measured productivity for the exposed patches 1, 2, 6 and 7 of replicate 1 in the landscape with atrazine application. The size of the symbols represents the local connectivity of the patch. The black line represents the values where the predictions equal the observations. The productivity was predicted using the measured toxicant concentration in the exposed patches by using Eq. 5.7 (triangles). By using a nonlinear squared model (Eq. 5.6), local connectivity was added as a predictor variable (circles), which generated a statistically significant better model fit.

Table 5.3. Result of the nonlinear squared model with the measured productivity of community 1, 2, 6, and 7 as response variables, and atrazine application and local connectivity as predictor variables. α , β and γ are the predicted values of the statistical analysis as represented in Eq. 5.6. p-values were corrected using the Bonferroni post-hoc test. * $p<0.0125$, ** $p<0.0025$, *** $p<0.00025$.

	patch 1		patch 2		patch 6		patch 7	
	Est	t-value	Est	t-value	Est	t-value	Est	t-value
α	0.009	0.82	0.009	1.04	0.012	1.11	0.007	0.47
β	2.522	14.19***	2.458	18.33***	2.784	11.16***	2.634	10.72***
γ	0.476	0.82	0.429	1.86	1.973	3.74*	1.426	2.93

The addition of local connectivity (as a measure of the number of connections per patch) as a predictor variable resulted in better model predictions of productivity (Fig. 5.3, circles) and the coefficient of local connectivity, β was always a significant predictor of productivity (Table 5.3). The analysis therefore shows that connectivity increased productivity through dispersal of algae rather than through a reduction of the atrazine concentration.

5.3.2 Diversity

On day 12, atrazine and connectivity did not affect regional diversity (Table 5.4, Fig. 5.4a). On day 30, atrazine marginally increased regional diversity and this positive effect increased when connectivity increased (Table 5.1, Fig. 5.4d).

The model predictions with connectivity as a first-order predictor did not significantly differ from the model predictions with connectivity as a second-order predictor (Appendix D Table D4). Therefore, only the results for the model predictions with connectivity as a first-order predictor are shown. On day 12, atrazine application did not affect diversity in the unexposed patches but increased diversity in the exposed patches (Table 5.4, Fig. 5.4b, c). Connectivity did not significantly affect diversity in the unexposed or exposed patches.

On day 30, atrazine application did not affect diversity in the unexposed patches but increased diversity in the exposed patches (Table 5.4, Figure 5.4 e, f). There were significant interaction effects between atrazine application and connectivity, indicating a positive effect of connectivity on the diversity of the unexposed patches in the landscapes with atrazine application. Moreover, a negative significant effect between atrazine application, connectivity and exposure indicates that connectivity decreased diversity in the exposed patches in the landscapes with atrazine application (Fig. 5.4 d, f).

5.3.3 Relative density

On day 12, atrazine and connectivity did not affect the relative density of DACT at a regional scale (Appendix D Table D6, Fig. D7). On day 30, atrazine application increased the relative density of DACT at a regional scale (Appendix D Table D6, Fig. D7). At a local scale, atrazine application and connectivity affected the relative density of DACT in a similar way as they affected diversity (Appendix D Table D6, Fig D7).

Table 5.4. Results of the generalized linear model with atrazine application, connectivity, their interaction and start day as predictor variables and the Shannon diversity as response variable. Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Day 12			Day 30		
	Value	SD	t-value	Value	SD	t-value
Intercept	0.0932	0.0113	8.27***	0.0037	0.0007	5.19***
Start day	-0.0341	0.0045	-7.64***	-0.0025	0.0006	-4.44***
Atrazine app	0.0110	0.0129	0.85	0.0078	0.0036	2.20*
Connectivity	-0.0002	0.0007	-0.28	0.0001	0.0000	1.13
Atrazine app x Connectivity	-0.0008	0.0008	-0.94	0.0005	0.0002	2.67*

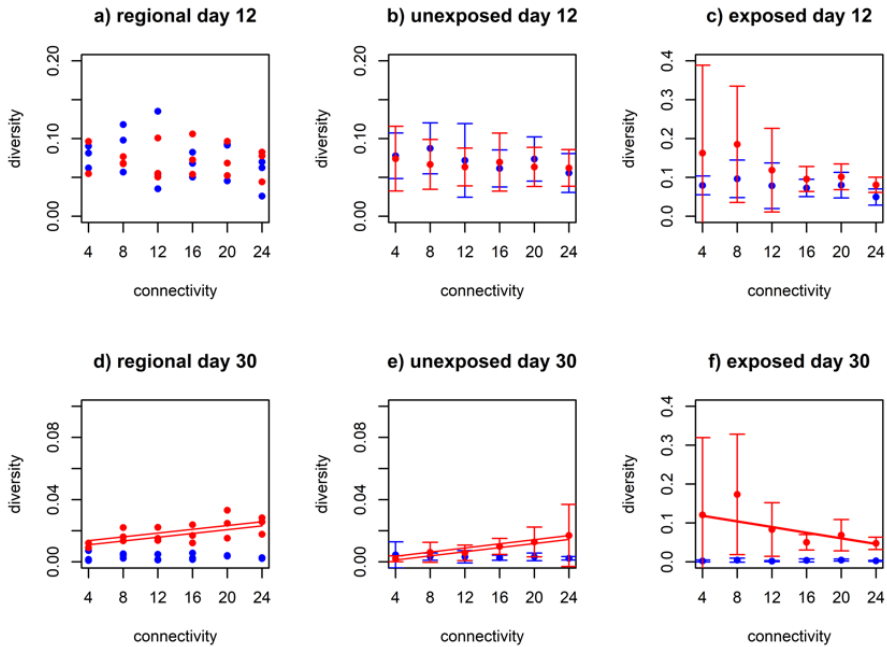


Figure 5.4. Shannon diversity vs. connectivity on days 12 and 30. Panels a and d represent the effect of connectivity on regional diversity in the control landscapes (blue) and the exposed landscapes (red) (3 replicates). Panels b and e represent the effect of connectivity on the local diversity of the unexposed patches in the control landscape (blue) and the landscapes with atrazine application (red) (mean \pm SD). Panels c and f represent the effect of connectivity on local diversity of the exposed patches in the control landscape (blue) and the landscapes with atrazine application (red) (mean \pm SD). The regression lines are only shown in case of a significant effect when using a mixed linear effect model (Table 5.4, Table 5.5).

Table 5.5. Results of the generalized linear model with connectivity, atrazine application (on a landscape level), patch exposure, their interactions and start day as predictor variables and local diversity on days 12 and 30 as response variable. Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Day 12			Day 30		
	Value	SD	t-value	Value	SD	t-value
Intercept	0.089	0.008	10.56***	0.004	0.001	5.15***
Start day	-0.038	0.006	-6.44***	-0.003	0.000	-5.46***
Atrazine app.	0.015	0.014	1.03	-0.002	0.002	-0.686
Patch exposure	0.019	0.010	1.87	-0.001	0.001	-0.841
Connectivity	0.000	0.001	0.101	0.000	0.000	1.556
Atrazine app x patch exposure	0.069	0.030	2.341*	0.131	0.023	5.60***
Atrazine app x connectivity	-0.001	0.001	-1.49	0.001	0.000	3.40***
Patch exposure x connectivity	-0.001	0.001	-1.48	0.000	0.000	1.04
Atrazine app x patch exposure x connectivity	-0.002	0.001	-1.44	-0.004	0.001	-3.73***

5.4 Discussion

5.4.1 Productivity

In contrast to what we expected (H1), connectivity increased regional productivity on day 12 in the landscapes with the chemical application. A positive effect of dispersal on productivity is usually found because of a spatial insurance effect when dispersal introduces stress-tolerant species that compensate for the productivity loss of stress-sensitive species (Thompson and Shurin 2012, Eggers et al. 2012, Symons and Arnott 2014, de Boer et al. 2014, De Raedt et al. 2016). In this study, connectivity did not introduce new species as local richness remained constant during the experiment. Instead, connectivity facilitated the redistribution of organisms from the unexposed to the exposed patches, compensating the negative effect of the chemical on local productivity in the exposed patches. However, in contrast to what we hypothesized, this redistribution did not generate a productivity loss in the unexposed patches on day 12 (H2). Probably, the dispersal-induced productivity loss was quickly compensated by the growth of the remaining algae during the three days between the manipulation of connectivity and sampling because the growth rate of the algae was near the exponential growth phase.

As hypothesized (H1), connectivity did not affect regional productivity on day 30 as the negative effect of connectivity in the unexposed patches was offset by the positive effect of connectivity in the exposed patches. We argue that the dispersal-induced loss of productivity could no longer be compensated by growth in the unexposed patches because algae were no longer in their exponential growth phase. Our results are in line with studies reporting no effect of dispersal on regional productivity in heterogeneous landscapes, while affecting the productivity of local patches (Lindström and Östman 2011, Smeti et al. 2016). Heterogeneity

in these other studies was caused by resources or natural variation and not by environmental stressors as we have done in the present study. Indeed, existing studies with environmental stressors have mostly focused on the population-level processes (Spromberg et al. 1998, Van den Brink et al. 2007, Brock 2013).

Some patches of the landscape remained more connected than others, which resulted in a strong variability of local productivity, especially at low connectivity (Fig. 5.2). Moreover, we found evidence that local connectivity showed a non-linear, saturating relationship with local productivity. Indeed, we found that the non-linear model, which predicted the effect of local connectivity on local productivity, showed better model residuals than the linear model (Eq. 5.6, Appendix D, Fig. D5). Moreover, the relationship between local connectivity and local productivity showed an overall saturating trend (Appendix D, Fig. D6, D8, D9). In other words, the removal of connections from a weakly connected patch decreased productivity more than the removal of connections from a highly connected patch. First, a higher number of connections decreased the difference in productivity between unexposed and exposed patches, reducing the contribution per connection to productivity. Second, when connectivity was low, not all exposed patches were connected to an unexposed patch. This shows that not only the number of connections, but also the landscape configuration (which patches remain connected) is important to predict local production. The importance of landscape configuration has been demonstrated before in landscapes where resources and patch sizes were manipulated (Carrara et al. 2012, 2014).

5.4.2 Diversity

The experimental results did not support hypotheses 3 and 4 (H3 and 4). Instead of decreasing regional diversity in landscapes where the chemical was applied, connectivity did not affect regional diversity on day 12 and increased regional diversity on day 30 (H3). Chemical application increased regional diversity by suppressing the competitive dominant species OD, allowing the subdominant but most stress-tolerant species DACT to persist in the exposed patches. As a result, OD dominated the unexposed patches and DACT dominated the exposed patches, fostering regional diversity and reflecting the trade-off between competitive strength and chemical tolerance. Because of this trade-off, DACT was almost entirely excluded in the unexposed patches, while OD could only persist in the exposed patches that were connected to unexposed patches.

We expected that connectivity would reduce regional diversity of the landscapes where the chemical was applied by benefitting the distribution of the regionally strongest competitor (Forbes and Chase 2002, Mouquet and Loreau 2003, Howeth and Leibold 2010b, Matthiessen et al. 2010a). However, we found that connectivity increased regional diversity on day 30.

Connectivity can increase regional diversity by increasing the relative density of a regionally subdominant species (Gilbert et al. 1998, Howeth and Leibold 2010a, Kneitel and Miller 2011, Seymour and Altermatt 2014). Our data showed that connectivity slightly benefitted the relative density of the regional subdominant species DACT (Appendix D Fig. D7). Probably, connectivity benefitted DACT as the dispersed organisms of DACT could persist longer in the unexposed patches than the dispersed organisms of OD could persist in the exposed patches. We found evidence for this in the isolated competition experiment where DACT lasted in the unexposed patches during the entire experiment, while OD was excluded after a few weeks in the exposed patches.

We found no evidence for hypothesis 4 that the relationship between connectivity and local diversity would be unimodal. Instead, we found that connectivity had a positive effect on the diversity of the unexposed patches, and a negative effect on the diversity of the exposed patches. This opposite effect was generated by a difference in productivity between the unexposed and exposed patches. Because of this difference in density, DACT was dispersed to the unexposed patch where the density of OD was high. In such conditions, the density of DACT was lower than the density of OD across all connectivity levels and connectivity thus increased local diversity in the unexposed patches. In contrast, OD was dispersed to the exposed patch where the density of DACT was low because of the high concentration of the chemical. A low connectivity enabled OD to persist in the exposed patches, generating a high local diversity. However, when connectivity increased, the relative density of OD progressively exceeded the relative density of DACT, which generated a strong dominance of OD and a reduction of local diversity. Because most studies manipulate heterogeneity by temperature, light or resources, which create gradients in productivity that are less strong than those created with a chemical stressor, such opposite effects of connectivity on local diversity within the same landscape are rarely reported (Davies et al. 2009, Matthiessen et al. 2010a, Carrara et al. 2014). This highlights the fact that the processes driving local and regional diversity in environmentally heterogeneous landscapes depend on which factor creates heterogeneity.

5.4.3 Limitations and conclusion

While the present study only contained two species that had a trade-off in competitive ability and stress sensitivity, most communities are defined by a higher species richness. Moreover, in this study, communities had an identical initial composition. However, in reality, stressors often occur in landscapes that have heterogeneous compositions because, among others environmental heterogeneity. Some patches might then contain more stress tolerant species than others and hence have a higher ability to limit stressor effects on productivity through shifts in composition. In such landscapes, dispersal might distribute stress-tolerant species among the landscape, limiting the effect of the stressor on regional productivity. For instance,

de Boer et al. (2014) created a light gradient among communities, and found that dispersal reduced the effect of heat stress on regional productivity by distributing a heat-tolerant species.

In this chapter, the positive effect of dispersal on the productivity of the exposed patches was not due to the increase of the density of the stress-tolerant species. Instead, dispersal increased the density of the stress sensitive-species. This mechanism also regulated how dispersal influenced the composition of exposed communities in several previous studies. For instance, Schriever et al. (2007) showed that the abundance of stress-sensitive species in exposed reaches remained high when connected to unexposed upstream reaches. Brock et al. (2010) and Schäfer et al. (2017) used an empirical and metapopulation model, respectively, to show that exposed insect populations recover more rapidly when organisms of stress-sensitive species can disperse from unexposed areas. These examples, together with others (Orlinskiy et al. 2015, Knillmann et al. 2018), show that the dispersal of stress-sensitive species to exposed patches is a common mechanism. As the proposed mechanisms in the present study show that connectivity strongly interferes with local effects of exposure events on community and ecosystem variables, we argue that ecosystem management and biodiversity conservation should adopt a landscape context.

6

Conclusion and perspectives

Environmental change drivers, such as global warming and chemical pollution increasingly challenge the earth's ecosystems. Today, the way these environmental changes affect the diversity and productivity of communities is an important subject of investigation (McMahon et al. 2012, Halstead et al. 2014, Mensens et al. 2015, De Laender et al. 2016, Spaak et al. 2017, Baert et al. 2018). This thesis contributed to this research by investigating the combined effect of stress and dispersal on the composition, diversity and productivity of communities (Fig. 6.1).

6.1 The combined effect of environmental stress and dispersal on composition, diversity and productivity

6.1.1 The combined effect of environmental stress and dispersal on composition and diversity

In this thesis, I studied the combined effect of environmental stress and dispersal in experimental communities of micro-algae. I found that the effect of dispersal on composition and diversity depended on the stress intensity.

In chapter 2, I showed that stress changed the effect of dispersal on composition by altering the composition and population density of the community to which the organisms immigrate. When those communities were unstressed, priority effects were strong and this resulted in a small dispersal effect on composition. When those communities were stressed, priority effects were low, and dispersal generated a strong shift in composition by introducing stress-tolerant species. Chemical environmental stress decreased priority effects because of two reasons. First, stress decreased growth rates, generating a higher resource availability for later-arriving species. Similar effects have been found in communities that were affected by disturbances through biomass removal (Gross et al. 2005, Symons and Arnott 2014). Second, stressors decreased priority effects through selection for a few tolerant species, which resulted in fewer possible community compositions. Similar effects have been found in communities that were repeatedly affected by drought, which selected for drought-resistant species (Chase 2007). Disturbance and drought are discrete events and the colonization success depends on the time between disturbance (or drought) and dispersal (Symons and Arnott 2014). In contrast, the concentration of a chemical stressor in my study remained relatively constant and the colonization success depended on the time between successive dispersal events as a longer time between dispersal events increased the time for early-arriving species to monopolize resources.

Table 6.1. General overview of the methodology and main results in the 4 research chapters of this PhD dissertation.

	Chapter 2	Chapter 3	Chapter 4	Chapter 5
Design	Microcosm experiment	Model simulations	Microcosm experiment	Microcosm experiment
Dispersal manipulation	3 levels, fixed densities from monocultures to communities	7 levels, fixed proportion between unexposed and exposed community	5 levels, fixed proportion between unexposed and exposed community	6 connectivity levels between 8 communities
Stressor manipulation	3 levels of chemical stress	6 levels of stress heterogeneity	4 Stressor flux levels	2 levels of stressor application
Stressor level	No/low stress	Unexposed	Unexposed	Unexposed
Main mechanisms	High stress Species sorting	Exposed Mass effects	Exposed No stressor flux: mass effect Stressor flux: compensation	Exposed Mass effects
Local diversity	Priority effects <i>Evenness</i> : negative	Mass effects <i>Richness</i> : hump > positive > negative	NA	Positive Negative
Local productivity	Negative	Positive NA	No stressor flux: negative Stressor flux: positive <i>beta-diversity</i> : negative	Negative Positive
Regional diversity	NA	NA		Positive
Regional productivity	NA	NA	No stressor flux: negative Stressor flux: positive	No effect

In chapter 3, I showed that the effect of dispersal on composition depended on differences between the stress intensity of the community to which organisms immigrate and on the stress intensity of the community from which the organisms emigrate. I defined this difference as stress heterogeneity. Stronger stress heterogeneity led to larger differences in composition and population density. As long as differences in population density were small, compositional differences increased the proportion of hump-shaped relationships between dispersal and diversity. However, when differences in composition and population density were large, no hump-shaped relationships appeared in the communities with a low stress-intensity because mass effects from the high-stressed community were too weak.

Hump-shaped relationships between dispersal and diversity have been predicted by several theoretical studies (Mouquet and Loreau 2003, Mouquet et al. 2006, Gilbert 2012) and the prevalence of such relationships is highest when heterogeneity is intermediate (Mouquet et al. 2006). Nevertheless, empirical studies that investigate how environmental heterogeneity affects diversity are rare. Most studies that investigate the effect of dispersal on diversity do so by using natural communities where heterogeneity is the consequence of natural variations and which have heterogeneous initial compositions (e.g. Gilbert et al. 1998, Collinge 2000, Severin et al. 2013, Berga et al. 2015). Although those experiments often find significant effects of dispersal on diversity (increase, decrease and hump-shapes), these set-ups do not allow to distinguish the effect of environmental heterogeneity from the effect of heterogeneous initial composition. A few studies have empirically studied the effect of environmental heterogeneity on diversity, often by manipulating heterogeneity by using only two levels (homogeneous vs heterogeneous environment) (for an overview of these studies, see Grainger and Gilbert 2016).

Mouquet et al. (2006) applied environmental heterogeneity by manipulating the spatial distribution of resources. Importantly, in their design, environmental heterogeneity increased differences in composition, but not in population density. Chapter 3 therefore represents an extension of the research by Mouquet et al. (2006) with spatial differences in both composition and population density. Moreover, I tested additional factor combinations i.e. interspecific variation in species response and initial compositions, which both increased the proportion of hump-shaped relationships.

The validity of trends predicted by the model must be tested with empirical studies. Unfortunately, such studies are lacking. Most studies that manipulated environmental heterogeneity did so by applying random disturbances (Matthiessen et al. 2010b, Altermatt et al. 2011a, 2011b). These removals reduce the average growth rate of the organisms, independent of species identity. This scenario is similar to one of the simulated scenarios from

chapter 3, namely the one where stress heterogeneity was high but the variation in niche mean and niche width was small. Therefore, disturbances create strong population density differences but only weak compositional differences. Consistent with the theoretical study in chapter 3, most of the empirical studies only report weak or no effects of dispersal on diversity (Altermatt et al. 2011a, 2011b), except when initial composition is heterogeneous (Matthiessen et al. 2010b). Other studies applied resource heterogeneity, which can generate differences in composition, but likely generates differences in population density that are smaller than those generated by stressors. Davies et al. (2009) created resource heterogeneity by adding different resources to patches, finding positive effects of dispersal on diversity in homogeneous and heterogeneous conditions. This result is in contrast with the present results as I predicted no significant relationships between dispersal and diversity in homogeneous environments when initial compositions are homogeneous. Other studies applied light gradients, which create different compositions, but often only low differences in population density (Matthiessen et al. 2010b, Eggers et al. 2012). These studies did not find effects of dispersal on diversity in homogeneous or heterogeneous environments.

To fully validate the simulation results, more studies are needed that investigate environmental heterogeneity by creating compositional and population density differences. Such information is crucial as many factors of environmental change, such as temperature and chemical stressors create substantial differences in population density and composition (Mensens et al. 2015, Spaak et al. 2017). As far as I know, only one study has manipulated temperature heterogeneity, showing the average growth rate to decrease with 35% and using species that showed different responses to a change in temperature (Limberger et al. 2014). However, this study did not find any dispersal effects on diversity, most likely because it only applied two dispersal levels.

In this thesis, I did not try to validate the theoretical results of chapter 3. However, I can test if the empirical results of chapter 5 are consistent with the theoretical results of chapter 3. In chapter 5, I exposed communities to different levels of chemical stress and manipulated dispersal by changing connectivity. The applied stressor concentration reduced the average growth rate of the species by approximately 60%. Moreover, species showed a different sensitivity towards the stressor as one species dominated the unexposed communities, while the other species dominated the exposed communities (Appendix D, Fig. D1.1). These conditions correspond to a large variation of the niche width and a small difference in niche mean. According to the theoretical model of chapter 3, these conditions would be likely to generate a hump-shaped relationship between dispersal and diversity in the exposed communities, but not in the unexposed communities. When I assume that the degree, which measures the number of connections arriving in/leaving a community, is a proxy for dispersal,

I can test how dispersal and local diversity relate in unexposed and exposed communities. The effect of degree on local diversity was tested by a linear and quadratic regression. For the exposed communities, the quadratic regression gave the best model fit (based on log likelihood), with significant coefficients for the first ($p = 0.045$) and second order ($p=0.024$) term, indicating a hump-shaped relationship between dispersal and diversity (Fig. 6.2a). In the unexposed communities, a linear regression gave the best model fit, showing dispersal to significantly increase diversity ($p < 0.001$) (Fig. 6.2b). This effect was very small because of the low density of the dispersed organisms. Thus, consistent to the simulations in chapter 3, the results from chapter 5 found a hump-shaped relationship between dispersal and diversity. However, the data from chapter 5 suggest a (albeit small) positive relationship between dispersal and diversity for the unstressed communities, while the theory from chapter 3 suggests that the probability for such a positive relationship is small.

These comparisons are the only way I could confront my theoretical results with empirical data but this comparison should be treated with caution. While the model assumed that dynamics were close to an equilibrium, the experimental communities were probably not. Indeed, the exclusion of subdominant species often takes long, which would have resulted in small stressor-induced changes in richness in the experiments. Hence, I used Shannon diversity as a measure for diversity in the empirical study. In contrast, the theoretical model used richness as a measure for diversity. Several empirical studies did not find strong effects of environmental heterogeneity on richness, while finding changes in evenness (Matthiessen et al. 2010a, Eggers et al. 2012, Mensens et al. 2015).

6.1.2 The combined effect of environmental stress and dispersal on productivity

Dispersal increased local productivity in two ways. First, in chapter 2, I demonstrated the potential for dispersal to increase productivity in the stressed communities when dispersal introduces stress tolerant species. These stress tolerant species increased productivity by compensating the stress-induced productivity loss, as predicted by the Spatial Insurance Hypothesis (Loreau et al. 2003a). Dispersal-induced changes in composition depend, among others, on which stressor is applied and the identity of the species in the regional species pool. I also found that the introduction of new species did not increase, but decreased productivity in the unexposed communities. The exact mechanism for this is unsure. Some new species that were introduced might have been poor competitors, decreasing the efficiency in which resources were consumed (Mouquet and Loreau 2003, Gilbert 2012).

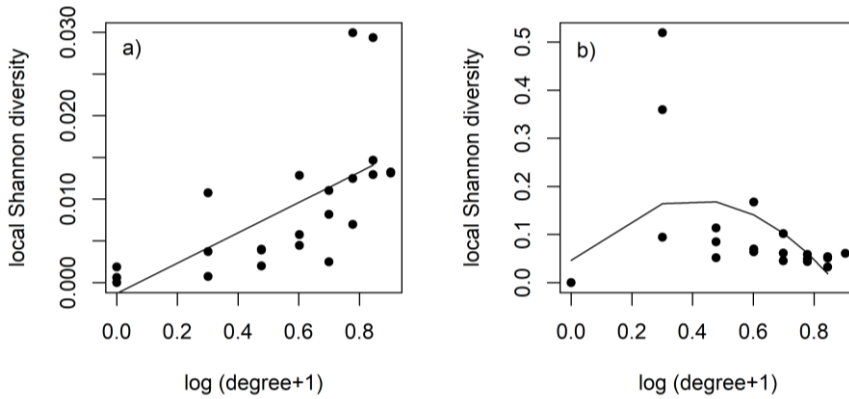


Fig. 6.2. Local Shannon diversity in function of the log transformed degree in the (a) unexposed and (b) exposed communities. Data were taken from chapter 5 from the landscapes with chemical application. Symbols represent the data. In (b) the symbol at (0,0) represents 3 overlapping data points. The line represents the (a) linear and (b) quadratic regression.

Second, when stress heterogeneity created differences in productivity, dispersal redistributed organisms from the unstressed communities, which had a high productivity, to the stressed communities, which had a low productivity. In chapter 5, the species that were introduced in the stressed communities could not persist without dispersal because most of the introduced species were very stress-sensitive. In chapter 4, the introduced species could persist in the stressed communities because the species that were introduced from the unstressed community were also most stress-tolerant. Nevertheless, under both conditions a high stressor concentration inhibited the growth of the introduced species. A redistribution had several effects on regional productivity. Dispersal had no effect on regional productivity when an increase in productivity of the stressed community resulted in a similar decrease of the productivity in the stressed community (day 30 in chapter 5). However, dispersal increased productivity when the removal of organisms from the unstressed community was rapidly compensated by local growth (e.g. day 12 in chapter 5). This mainly occurred when species were in the exponential growth phase. Last, dispersal decreased regional productivity when it moved the best adapted species from the unstressed community to the stressed community, as occurred in chapter 4 (day 24). Such negative effects on regional productivity have mainly been found from model simulations assuming that dispersal introduces poor competitors or when dispersal removes the best-adapted species (Mouquet and Loreau 2003, Gilbert 2012). Empirically, negative effects are mainly demonstrated at high dispersal rates (Howeth and Leibold 2010a, Lindström and Östman 2011).

6.1.3 Material fluxes

In chapters 2, 3 and 5, stressor concentrations remained relatively stable during the experiment. However, in reality, stressor concentrations can change because of stressor fluxes. In chapter 4, I showed that a stressor flux increases the positive effect of dispersal on regional productivity because of increased compensatory dynamics. Material fluxes have been shown before to change the productivity of communities (Gounand et al. 2017, Harvey et al. 2017, Limberger et al. 2017). Fluxes can redistribute resources between communities, supplying nutrients for autotroph organisms, while supplying organic material for heterotrophic organisms (Gounand et al. 2017). Moreover, the combination of dispersal and material fluxes are shown to affect ecosystem functions differently than when material fluxes occur alone (Limberger et al. 2017). However, the combination of material fluxes and dispersal was hardly studied before by manipulating both fluxes independently. So far, only one study has done so, showing that a strong material flux can suppress the dispersal of organisms by disrupting local dynamics in the source community (Harvey et al. 2016). However, this study did not look at interaction effects between dispersal and the stressor flux on productivity. The study in chapter 4 was therefore the first that showed that the effect of dispersal on productivity can change when manipulating a material flux.

6.1.4 Network structure

In chapter 2 until 4, I investigated the combined effect of environmental stress and dispersal on diversity and productivity in two-patch metacommunities. However, real landscapes are spatially extended, containing multiple patches (Davies et al. 2009, Carrara et al. 2012, 2014). Many of those landscapes are subject to decreasing connectivity through habitat destruction and increasing fragmentation (Pimm and Raven 2000) and it is unsure how results obtained in simple two-patch metacommunities would apply to this more complex reality. In chapter 5, I investigated the effect of connectivity on diversity and productivity in landscapes that were exposed to a chemical stressor by manipulating the number of connections among patches. Manipulating connectivity generates effects on diversity and productivity that do not appear when manipulating dispersal rates in two-patch metacommunities. First, at a low connectivity, I found a strong difference in productivity and diversity among patches within the same landscape, even when those patches had equal stressor concentrations. This confirms the results of earlier studies that showed that not only the environmental conditions, but also the position of a patch within a landscape affects its diversity and productivity (Carrara et al. 2012, 2014). Second, the saturating relationship between local connectivity and productivity in chapter 5 demonstrated that the removal of connections from highly-connected patches induced smaller effects on productivity than the removal of connections from weakly-connected patches. The study chapter 5 thus showed that not only the number of connections

but also the identity of the removed connections matters for the subsequent effects on the diversity and productivity of patches. Transferring the results to communities in real aquatic landscapes is difficult, because of the simple model system that I used. Nevertheless, the present study suggests that even a low degree of connection between exposed streams in agricultural areas and more pristine streams might already considerably increase the abundance of stress-sensitive species compared to isolated conditions.

6.2 Limitations and perspectives

6.2.1 Species interactions

In this dissertation, I only used species that belong to the taxon of the marine diatoms (*Bacillariophyceae*). Because those species have a high resource use overlap, competition in diatom communities is generally high, leading to the exclusion of most species (Bruno et al. 2003, Giller et al. 2004, Baert et al. 2016a). For instance, in chapter 4, only 3 out of 6 species remained present during the entire experiment. Because of, among others, niche partitioning and facilitative interactions, most real communities contain a much higher number of species than the experimental communities in this thesis. In such more diverse communities, the number of potentially dispersing species is greater.

I only incorporated one trophic level in the study systems. Nevertheless, the presence of an additional trophic level can change the effect of dispersal on other trophic levels. For example, predation is shown to reduce the effect of prey dispersal on prey diversity (Chase et al. 2010, Howeth and Leibold 2010a, Kneitel and Miller 2011). However, these results are not consistent as predation did not change the effect of dispersal on diversity or productivity in several other empirical studies (Cadotte et al. 2006a, Berga et al. 2015). Moreover, dispersal-diversity and dispersal-productivity relationships potentially differ among trophic levels (Howeth and Leibold 2010a, Anstrom and Part 2013). For instance, dispersal is empirically demonstrated to increase the abundance of predators by increasing predator richness, while decreasing the abundance of prey (Chase et al. 2010). The variation in empirical results indicates that the mechanisms linking food-web dynamics with spatial dynamics needs further attention, especially in heterogeneous environments (Massol et al. 2017). Chemical stressors can be a useful group of stressors to apply in such studies. Many chemical stressors only target one trophic level. For instance, photosystem-inhibiting herbicides target algae and plants (Halstead et al. 2014, De Laender et al. 2016). Consequent changes in composition on the lowest trophic level might generate indirect negative effects on higher trophic levels because of a lower food availability (Brock et al. 2000, Fleeger et al. 2003). In this thesis, I showed that dispersal might mitigate the negative effects of chemical stress on one trophic level. A subject of investigation should then be if dispersal is also able to mitigate the indirect

effects of chemical stressors on higher trophic levels. Moreover, it would be interesting to examine if different dispersal rates among trophic levels would influence the results.

6.2.2 Dispersal method

In all chapters of this dissertation, dispersal was performed using bulk dispersal. This implies that the number of individuals that dispersed among communities depended on the species abundances, i.e. is positive density dependent (except in chapter 2 where all species had an equal dispersal probability). Such an approach is the most-used experimental design to test dispersal-diversity relationships as it facilitates tractability (for a review, see Grainger and Gilbert 2016). Bulk dispersal generates species sorting and mass effects which have been shown to be the main drivers of community assembly processes in landscapes where dispersers move passively (Cottenie 2005, Soininen 2014). However, a different dispersal ability among species can generate coexistence mechanisms that do not occur with bulk dispersal (Melián et al. 2015). First, an interspecific variation in dispersal ability can generate competition-colonization trade-offs (Yu and Wilson 2001, Cadotte et al. 2006b). For instance, Matthiessen and Hillebrand (2006) allowed micro-algae species to disperse among communities and found that diversity was highest at an intermediate dispersal rate when both efficient colonizers and good competitors were present. Stressors can disrupt colonization-competition trade-offs. For instance, chemical stressors can decrease the competitive ability of the best competitor, benefitting the best colonizer. In contrast, chemical stressors can also hinder the movement of the best colonizer, as has been shown with daphnids and arthropods (Dodson and Hanazato 1995, Desneux et al. 2007). A reduced movement can benefit the best competitor, decreasing regional coexistence.

Several studies have shown that dispersal varies with environmental contexts such as resource availability (e.g. Kennedy and Ward 2003, Pennekamp et al. 2014, Fronhofer et al. 2015b, 2018), intraspecific densities (e.g. Baines et al. 2014, Pennekamp et al. 2014, Fronhofer et al. 2015a), and interspecific interactions (e.g. Bestion et al. 2014, Fronhofer et al. 2015b, Tanaka et al. 2016). Also chemical stressors are demonstrated to affect the movement of organisms. Many organisms, such as fish, amphibians, molluscs and cladocerans show an avoidance behavior when exposed the chemical stressors, even at sub-lethal levels (Araújo et al. 2016). In chapter 5, I showed that dispersal might decrease the negative effect of chemical stress on species abundances by moving organisms from the unexposed to the exposed communities. However, such movement is expected to be limited when organisms move actively away from exposed communities. As such, positive effects of dispersal on composition and productivity might be lower than expected from the experiments. Moreover, dispersal might increase the effect of a chemical stressor on composition and productivity when organisms emigrate from the exposed communities. Further research

should investigate how chemicals affect the behavior of organisms and how this might cause changes in the way dispersal affects diversity and productivity.

6.2.3 Stressors

While I applied only one chemical stressor in this thesis, real communities are often exposed to multiple chemical stressors simultaneously (De Laender 2018). For instance, Deschutter et al. (2017) measured several PAH's and PCB's in water samples in the North Sea. Although only low concentrations were recorded, mixtures of these chemicals might have strong species and community-level effects (Deschutter et al. 2017, Nys et al. 2018). Applying mixtures of chemicals, preferably at environmental concentrations, should therefore be a next step in assessing how dispersal and chemical stress interact in communities.

Next to chemical stressors, communities are also exposed to several other types of stressors such as salt stress, temperature change or drought. The occurrence of multiple stressors can decrease the capacity of species from the local or regional species pool to compensate for stressor-induced losses in productivity because not enough taxa might be able to withstand multiple stressors (Thompson and Shurin 2012). Under such conditions, positive effects of dispersal on productivity through species sorting might be low and mass effects from unexposed to exposed communities might be more important than when only one stressor would be present.

The stress gradient hypothesis predicts that increasing stress levels increase the number of facilitative interactions. So far, there is no evidence that herbicides might increase facilitative interactions in marine micro-algae communities (Baert et al. 2016a). However, other stressors such as drought are demonstrated to increase facilitative interactions (Grime 1973, Maestre et al. 2009). When competitive interactions shift to facilitative interactions, local richness might increase (Yang et al. 2015), while also productivity might increase through higher complementarity effects (Baert et al. 2018). Hence, the contribution of dispersal for maintaining diversity and increasing productivity might be less than when no shift from competition to facilitation occurs. In the future, it might hence be worth to test the effect of dispersal in communities that are exposed to different types of stressors.

6.2.4 Material fluxes

I showed that a combined stressor flux and dispersal generated compensatory dynamics. Future studies could investigate if dispersal generates compensatory dynamics with other types of fluxes, such as fluxes of resources. Stressors and resources differ as stressor levels are mostly not affected by organisms, while resource levels are. Therefore, resources can move among patches through a resource flux and through the dispersal of organisms (Haegeman and Loreau 2014, Massol et al. 2017).

In chapter 4, I investigated how dispersal affected beta-diversity along a stressor flux gradient. However, I did not investigate how dispersal and a stressor flux combine in affecting local or regional diversity. It has been theoretically demonstrated that resource fluxes can increase the homogenizing effect of dispersal on community composition, decreasing local and regional diversity (Haegeman and Loreau 2014) but experimental validation for this is still lacking.

6.2.5 Spatial extension of the landscape

Until now, most experiments investigated the effect of dispersal in simple two- or three-patch metacommunity systems by manipulating the dispersal rate between patches (Grainger and Gilbert 2016). I used a similar approach in chapters 2, 3 and 4. In chapter 5, I applied a different method by manipulating the number of connections among communities. In this chapter I did not distinguish structural from functional connectivity. Indeed, the movement of organisms does not only depend on the physical presence of connections, but also on the needs, perception, and the response norms of the organisms (Nathan et al. 2008). For instance, an increasing number of connections might not improve dispersal when the organism avoids habitat edges. More studies are needed to assess how connectivity affects dispersal in real landscapes.

In chapter 5, I defined connectivity as the number of connections in a landscape. However, there are multiple ways to define connectivity. For instance, the maximum distance between patches is another possible measure of connectivity (Kindlmann and Burel 2008). Future studies could also investigate several other extensions. First, such studies could test how the spatial distribution and spatial average of stressor levels affect diversity and productivity. In chapter 5, I only used two different levels of the chemical, which was randomly distributed over the landscape. Second, future studies could ask how the appearance of new connections combines with the loss of other connections. Third, environmental change might remove patches instead of connections and so future studies could focus on this alternative form of fragmentation. Importantly, the order in which patches are removed will be an important factor in such studies (Thompson et al. 2016).

6.3 Consequences for the ecological risk assessment of chemicals

6.3.1 Effect of dispersal in exposed communities

In this dissertation, I exposed marine micro-algae of the class *Bacillariophyceae* (diatoms) to the photosynthesis inhibiting herbicide atrazine. EC_{50} values of the species varied between $53 \mu g\ l^{-1}$ and $480 \mu g\ l^{-1}$. A similar variation in sensitivity towards atrazine is found in other micro-algae studies (Debelius et al. 2008, Sjollema et al. 2014, Wood et al. 2014). Such variation in sensitivity towards atrazine can create shifts in composition when stress-sensitive species are replaced by more stress-tolerant species (e.g. in micro-algae community experiments: Seguin et al. 2001, Herman et al. 2011). Such compositional changes were also observed in chapter 2 of this dissertation. Moreover, I showed that sensitive species may not only be replaced by less-sensitive local species, but also by less-sensitive species from the regional species pool. The introduction of species from the region generated strong compositional turnovers that often exceeded the compositional changes under isolated conditions (Appendix A Fig. A1.2). Therefore, a compositional turnover in communities that are exposed to chemical stressors might be stronger in open communities than expected from (isolated) community experiments.

In chapter 4 and 5, I showed that dispersal might reduce the effect of a chemical stressor in exposed communities by moving stress-sensitive species from the unexposed communities (chapter 4, chapter 5). Positive effects of dispersal on populations that are exposed to chemicals have been found in several metapopulation models (e.g. Spromberg et al. 1998, Galic et al. 2012a, Willson and Hopkins 2013, Focks et al. 2014, Schäfer et al. 2017), field studies (Schriever et al. 2007, Orlinskiy et al. 2015, Knillmann et al. 2018) and a mesocosm experiment (Brock et al. 2010). The dispersal of sensitive species from unexposed to exposed communities can have important implications for risk assessment in exposed communities. First, species sensitivities may overestimate chemical effects in landscapes because they do not consider rescue from unexposed areas of the landscape. Second, bio-indicators such as *SPEAR_{pesticides}* might underestimate the impact of pesticide contamination as abundances of dispersed organisms are higher than where no dispersal would be present (Knillmann et al. 2018). Furthermore, the dispersal of sensitive species from unexposed to exposed communities can also have important implications in the unexposed communities. Indeed, in chapters 4 and 5 the density of the locally most competitive species often decreased in the unexposed communities. Such negative effects have been predicted before in several metapopulation models (e.g. Spromberg et al. 1998, Schäfer et al. 2017) and in a mesocosm experiment (Brock et al. 2010). Ecosystems that are hence protected because of their high value (e.g. in terms of the services they provide) may still be affected indirectly by chemicals that are present in nearby patches. The extent to which dispersal affects the density of

organisms in the unexposed or exposed patches depends on, among others, the duration or frequency of chemical exposure. For instance, Schäfer et al. (2017) found stronger effects of dispersal on population abundances in unexposed and exposed patches under repeated exposure pulses than after a single exposure pulse. In this dissertation, the concentration of the chemical stressor remained constant during the entire experiment (except in the presence of a stressor flux in chapter 4) which probably resulted in stronger and more long-term effects than would have occurred under a pulse exposure.

In contrast to most studies that investigated the effect of dispersal in communities exposed to chemicals, I also evaluated the effect of dispersal and chemical stress on diversity and productivity. While chemicals often decrease local diversity by excluded stress-sensitive species (Relyea 2005, McMahon et al. 2012, Muturi et al. 2017), I have shown that chemicals potentially increase diversity at a regional scale (chapter 5). Although maintaining diversity is a major objective within conservation biology, the increase of the abundance of stress-tolerant species may have detrimental effects on ecosystem functions (Spaak et al. 2017). For instance, algae groups may respond differently to herbicide exposure (Lockert et al. 2006) and harmless algae such as diatoms and green algae may be replaced by toxic algae such as cyanobacteria (Ma 2005).

Effects of chemical stressors on productivity often appear at a lower concentration than on diversity (Mensens et al. 2015, Spaak et al. 2017). I found that dispersal might reduce the negative effect of stress by introducing stress-tolerant species that compensate the stressor-induced productivity loss, or by introducing stress-sensitive species from unexposed areas. However, both mechanisms have drawbacks: when stress-tolerant species disperse from the region to an exposed community, dispersal might be detrimental for composition by generating strong changes in composition. Moreover, when dispersal introduces stress-sensitive species that are locally inhibited by the stressor, dispersal might generate an indirect effect on the composition and productivity of the unexposed communities. This generates strong implications for the protection goals that should be pursued (i.e. protection of composition or productivity), as well as which communities should be protected.

6.3.2 Effect of dispersal with chemical dilution

Exposure to chemicals often occurs in short pulses because degradation or dilution reduces the concentration of the chemical after application. In chapter 4, the stressor flux between the unexposed and exposed community diluted the chemical. This dilution decreased the concentration of the chemical in the exposed community and generated a partial recovery in that community. Here, I define recovery relative to the species densities and community productivity in unexposed and isolated conditions. Numerous studies have shown that

populations and communities can recover after the exposure to a chemical stressor (e.g. Van Den Brink et al. 1996, Laviale et al. 2011, Proia et al. 2011). The probability and time needed for recovery depend on many factors, such as the time of exposure (Gustavson et al. 2003), species life cycles (Van Den Brink et al. 1996, Gustavson et al. 2003) and initial diversity (Baert et al. 2016b). Some studies found no recovery at all (Lawrence et al. 2015), which might occur when chemical stress drives species to exclusion (Mcmahon et al. 2012). An important mechanism that can increase recovery is the supply of organisms from the region (Caquet et al. 2007, Trekels et al. 2011, Galic et al. 2012a, Focks et al. 2014). In chapter 4, I showed that dispersal increased the rate of recovery in the exposed community in the presence of a stressor flux. A stress-tolerant species was introduced from the unexposed community and facilitated recovery when the chemical was redistributed over the meta-ecosystem. However, it should be noted that full recovery was never achieved in the exposed communities because species composition in the exposed communities remained different from species composition in the isolated unexposed communities. Moreover, because of the stressor flux, the concentration of the chemical stressor increased in the unexposed community, affecting the composition and productivity in that community. The extent to which a stressor flux changes productivity and composition in the initially unexposed and exposed communities depends on the dose response curves of the species. In chapter 4 for instance, species' carrying capacities increased more when the stressor concentration in the initially exposed community decreased than the species' carrying capacities decreased when the stressor concentration in the initially unexposed community increased.

The community conditioning hypothesis states that communities retain information about events in their history e.g. regarding chemical exposure. This hypothesis is derived from the demonstration that communities are not at equilibrium, but rather are in the process of responding to their own unique history of interactions (Matthews et al. 1996). After a toxicant pulse in one community, differences in community composition and productivity may therefore persist when the chemical stressor is completely homogenized among initially unexposed and exposed communities. In chapter 4, the chemical stressor was close to complete homogenization at the end of the experiment. Differences in composition and productivity between the initially unexposed and exposed community were still visible, as changes in productivity and composition under a stressor flux occurred slowly. However, dispersal reduced differences in composition and productivity between initially unexposed and exposed communities. Indeed, dispersal generates interactions between organisms that originate from different communities and might hence decrease community conditioning. Long-term experiments are needed to demonstrate how long the community conditioning contributes in affecting composition and productivity after chemical exposure.

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A

Supporting information for chapter 2

Appendix A1. Tables and Figures

Table A1.1. Species strains and biovolume

Number	Species	Volume (μm^3)	Number	Species	Volume (μm^3)
1	<i>Thalassiosira</i> sp.	56886	7	<i>Bacillaria</i> sp.	7880
2	<i>Ditylum brightwelli</i>	24757	8	<i>Guinardia</i> sp.	14002
3	<i>Thalassiosira</i> sp.	2800	9	<i>Thalassiosira</i> sp.	12557
4	<i>Asterionella</i> sp.	1346	10	<i>Thalassiosira</i> sp.	25727
5	<i>Odontella</i> sp.	7520767	11	<i>Thalassiosira</i> sp.	102909
6	<i>Pseudo-nitzschia</i> sp.	3940	12	<i>Coscinodiscus</i> sp.	367008

Table A1.2. Initial species

Day 0				
A	11	1	9	4
B	12	7	4	6
C	1	6	10	9
D	5	11	7	3
E	8	2	9	5

Table A1.3. Dispersal sequence for low dispersal

	Day 7				Day 14				Day 21			
A	2	1	5	7	6	4	10	8	3	12	9	8
B	10	4	12	9	5	2	3	8	12	10	8	11
C	12	9	3	7	4	10	11	6	4	2	8	5
D	5	11	4	8	12	5	9	4	2	6	8	5
E	4	9	11	12	11	9	6	5	9	7	1	6

Table A1.4. Dispersal sequence for high dispersal

	Day 3				Day 7				Day 10				Day 14				Day 17				Day 21				Day 24			
A	5	6	1	5	6	1	5	6	1	5	6	1	10	6	9	12	12	5	7	11	2	4	3	8	2	5	6	4
B	9	8	10	9	8	10	9	8	10	9	8	10	3	11	5	12	11	1	9	7	9	12	11	5	11	8	6	10
C	10	4	12	10	4	12	10	4	12	10	4	12	8	6	3	5	7	1	12	9	1	11	8	7	4	8	9	3
D	4	7	1	4	7	1	4	7	1	4	7	1	6	5	10	12	10	4	11	9	2	1	9	8	11	10	9	4
E	8	10	1	8	10	1	8	10	1	8	10	1	10	8	1	3	12	8	1	6	10	7	11	2	3	9	12	8

Table A1.5. Nutrient concentrations. NA not measured.

Day	Composition	Dispersal	Stress (ppb)	PO_4^{3-} ($mg\ l^{-1}$)	NO_3^- ($mg\ l^{-1}$)	($Si\ \mu g\ l^{-1}$)
7	1	no	0	1.2424	35.51	3.86
7	2	no	0	1.8806	41.98	0.89
7	3	no	0	1.2316	34.86	3.01
7	4	no	0	1.6796	41.42	4.15
7	5	no	0	1.432	43.77	1.081
7	1	low	0	0.7812	33.93	0.22
7	2	low	0	1.8346	37.73	1.24
7	3	low	0	1.1434	29.23	1.34
7	4	low	0	1.8358	42.79	2.61
7	5	low	0	1.885	49.68	1.227
7	1	high	0	0.6086	32.23	0.12
7	2	high	0	1.5744	37.89	0.96
7	3	high	0	1.3784	36.07	5.71
7	4	high	0	1.9971	38.87	2.09
7	5	high	0	1.89	49.43	1.221
14	1	no	0	0.2766	22.71	0
14	2	no	0	NA	NA	NA
14	3	no	0	0.5342	29.07	1.39
14	4	no	0	NA	NA	NA
14	5	no	0	0.1714	0.348	0.49
14	1	low	0	0.366	23.08	0
14	2	low	0	NA	NA	NA
14	3	low	0	<0.2	27.09	1.91
14	4	low	0	NA	NA	NA
14	5	low	0	<0.2	17.57	1.15
14	1	high	0	<0.2	22.31	0
14	2	high	0	NA	NA	NA
14	3	high	0	<0.2	13.44	0.05
14	4	high	0	NA	NA	NA
14	5	high	0	<0.2	14.86	1.23
21	1	no	0	<0.2	29.27	0.54
21	2	no	0	1.4307	39.19	1.08
21	3	no	0	0.6804	24.78	0
21	4	no	0	0.2759	25.47	0.6
21	5	no	0	<0.2	4.53	0.48
21	1	low	0	<0.2	11.74	0.25
21	2	low	0	1.4393	38.54	1.13
21	3	low	0	0.8146	30.32	0.69
21	4	low	0	0.1896	25.83	0.48
21	5	low	0	<0.2	12.35	0.24
21	1	high	0	<0.2	8.06	0.5
21	2	high	0	1.0987	33.97	1.17
21	3	high	0	1.1069	30.12	0.06
21	4	high	0	<0.2	16.03	0.84
21	5	high	0	<0.2	2.79	0.11
28	1	no	0	<0.2	24.41	0.1
28	2	no	0	0.5714	41.54	0.01

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28	3	no	0	0.3622	22.43	0.15
28	4	no	0	0.23	24.7	0.45
28	5	no	0	0.252	1.21	0.3
28	1	low	0	<0.2	12.83	0.1
28	2	low	0	0.3733	36.32	0.29
28	3	low	0	0.9356	NA	NA
28	4	low	0	0.7755	33	0.28
28	5	low	0	0.138	3.98	0.3
28	1	high	0	0.9116	23.16	0.06
28	2	high	0	0.6275	30.73	0.03
28	3	high	0	1.085	36.84	0.11
28	4	high	0	NA	NA	NA
28	5	high	0	0.063	8.91	0.11
28	1	no	25	<0.2	13.16	0.28
28	2	no	25	0.6432	33.36	0.49
28	3	no	25	0.2967	22.67	0.34
28	4	no	25	<0.2	21.62	0.43
28	5	no	25	0.2224	4.94	0.14
28	1	low	25	0.5059	19.07	0.19
28	2	low	25	1.1359	37.53	0.21
28	3	low	25	1.3104	33.08	0.16
28	4	low	25	0.2722	13.97	0.21
28	5	low	25	0.1147	10.69	0.03
28	1	high	25	1.0502	24.53	0.09
28	2	high	25	NA	NA	NA
28	3	high	25	1.2014	35.99	0.06
28	4	high	25	0.2476	21.21	0.29
28	5	high	25	0.0762F	6.32	0
28	1	no	250	2.4652	46.28	9.07
28	2	no	250	1.3224	42.55	0.61
28	3	no	250	1.5763	41.7	1.33
28	4	no	250	1.9795	51.58	0.08
28	5	no	250	2.692	45.18	13.08
28	1	low	250	2.4652	41.66	3.78
28	2	low	250	1.3224	34.86	0.44
28	3	low	250	1.5763	31.7	0.27
28	4	low	250	1.9795	40.89	0.44
28	5	low	250	1.9801	45.34	3.51
28	1	high	250	0.9998	31.01	0.26
28	2	high	250	0.7195	30.4	0.14
28	3	high	250	0.7065	26.32	NA
28	4	high	250	1.1057	31.21	0.39
28	5	high	250	1.1535	32.27	0

Table A1.6. Results of the generalized linear model of the relative abundances at no dispersal using stress as predictor variable.

	Intercept		Low stress		High stress	
	mean±sd	p	mean±sd	p	mean±sd	p
1	-2.80 ± 0.37	<0.001	0.34 ± 0.024	0.495	-1.07 ± 0.71	0.154
2	-3.39 ± 0.48	<0.001	0.26 ± 0.64	0.704	-6.81 ± 17.06	0.706
3	-0.45 ± 0.62	0.493	-0.63 ± 0.93	0.524	-0.00 ± 0.87	0.998
4	-1.12 ± 0.40	0.011	-0.30 ± 0.60	0.608	-13.62 ± 264.30	0.960
5	-0.55 ± 0.69	0.444	0.99 ± 0.58	0.114	-7.20 ± 9.64	0.468
6	-0.91 ± 1.76	0.611	0.29 ± 0.29	0.333	1.32 ± 0.32	<0.001
7	-2.93 ± 0.63	<0.001	0.44 ± 0.81	0.599	3.39 ± 0.69	<0.001
8	-7.86 ± 2.80	0.038	-8.45 ± 185.6	0.965	11.57 ± 2.80	0.010
9	-1.97 ± 0.75	0.015	-0.93 ± 0.50	0.080	-1.75 ± 0.71	0.023
10	-2.03 ± 0.29	0.915	-0.63 ± 0.48	0.242	-1.64 ± 0.67	0.051
11	-0.12 ± 1.09	0.123	-0.313 ± 0.66	0.640	-0.078 ± 0.65	0.907
12	2.67 ± 0.37	<0.001	0.19 ± 0.55	0.737	-3.77 ± 0.43	<0.001

Table A1.7. Results of the generalized linear model of the absolute abundances at no dispersal using stress as predictor variable.

	Intercept		Low stress		High stress	
	mean±sd	p	mean±sd	p	mean±sd	p
1	4.28 ± 4.28	<0.001	0.05 ± 0.63	0.936	-3.32 ± 0.627	<0.001
2	4.40 ± 0.35	<0.001	0.31 ± 0.26	0.290	-5.01 ± 0.291	<0.001
3	5.10 ± 0.31	<0.001	0.04 ± 0.24	0.877	0.00 ± 0.242	0.986
4	2.60 ± 1.56	0.117	0.12 ± 0.93	0.895	-4.47 ± 0.929	<0.001
5	4.72 ± 0.89	<0.001	0.42 ± 0.91	0.655	-3.74 ± 0.960	<0.001
6	4.81 ± 0.46	<0.001	-0.03 ± 0.87	0.333	-0.26 ± 0.160	0.127
7	3.68 ± 0.67	<0.001	0.32 ± 0.28	0.274	1.53 ± 0.284	<0.001
8	0.39 ± 1.51	0.805	-1.25 ± 1.12	0.315	3.44 ± 1.25	0.0401
9	3.97 ± 0.85	<0.001	-0.59 ± 0.96	0.543	-1.86 ± 0.987	0.074
10	4.55 ± 0.41	<0.001	-0.40 ± 0.32	0.250	1.44 ± 0.317	0.004
11	5.20 ± 0.77	<0.001	0.01 ± 0.70	0.988	-2.20 ± 0.700	0.007
12	5.44 ± 0.08	<0.001	0.15 ± 0.062	0.052	-0.74 ± 0.0624	<0.001

Table A1.8. Results of the linear regression model using a logit function for stress, dispersal, the square root of day of introduction (Dol) and their interactions on the relative abundance of seven species.

Factor	Species 1	Species 5	Species 6	Species 7	Species 10	Species 11	Species 12							
Intercept	-0.477±0.587	0.419	-1.606±0.402	<0.001	-1.046±0.721	0.151	-1.363±1.149	0.2394	1.23±1.20	0.311	-0.636±0.161	<0.001	1.224±0.707	0.088
Low stress	0.212±0.178	0.236	1.662±0.448	<0.001	0.220±0.344	0.525	-1.620±0.386	<0.001	-2.61±0.46	<0.001	0.003±0.200	0.987	1.594±0.793	0.048
High stress	-2.934±0.424	<0.001	-1.743±0.795	0.031	0.335±0.335	0.3206	1.873±0.261	<0.001	-6.67±1.31	<0.001	-2.676±0.397	<0.001	-0.997±0.569	0.084
High dispersal	-0.542±0.175	0.003	-0.658±0.342	0.058	0.473±0.318	0.141	-2.271±0.487	<0.001	-1.15±0.37	0.003	-0.616±0.186	0.002	0.394±0.444	0.378
Dol	-1.172±0.234	<0.001	-0.577±0.235	0.016	-1.148±0.251	<0.001	-1.797±0.560	0.002	-1.97±0.36	<0.001	-1.677±0.388	<0.001	-1.146±0.242	<0.001
Low stress x Dol	0.614±0.221	0.007	-0.457±0.316	0.153	0.037±0.178	0.835	0.987±0.363	0.008	0.70±0.23	0.004	0.612±0.418	0.147	-0.314±0.272	0.253
High stress x Dol	0.540±0.221	0.031	0.676±0.335	0.047	0.280±0.157	0.079	0.421±0.313	0.183	0.37±0.46	<0.001	1.473±0.420	0.001	1.048±0.195	<0.001
High dispersal x Dol	-	-	-	-	-	-	0.902±0.437	0.043	1.65±0.33	0.007	-	-	-	-
Low stress x high dispersal	-	-	-	-	-0.222±0.428	0.606	1.645±0.737	0.029	-	-	-	-	-1.231±0.629	0.054
High stress x high dispersal x Dol	-	-	-	-	0.830±0.399	0.041	1.993±0.539	<0.001	-	-	-	-	-1.399±0.530	0.014
Low stress x high dispersal	-	-	-	-	-	-	-1.653±1.103	0.139	-	-	-	-	-	-
Low stress x high dispersal x Dol	-	-	-	-	-	-	-0.805±0.452	0.079	-	-	-	-	-	-

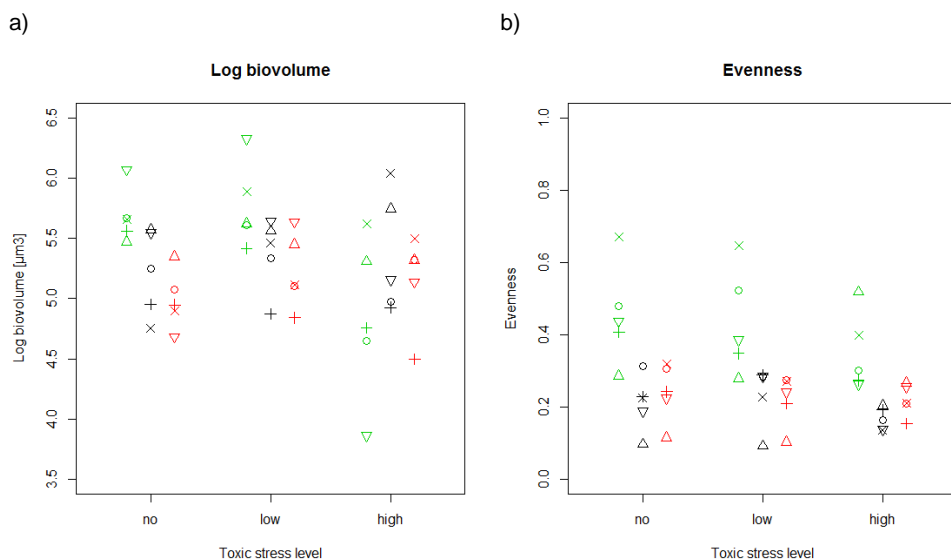


Fig. A1.1. Log final biovolume (a) and evenness (b), separated according composition, in function of stress level. O composition A, Δ composition B, + composition C, x composition D, ∇ composition E. Green: no dispersal, black: low dispersal, red: high dispersal.

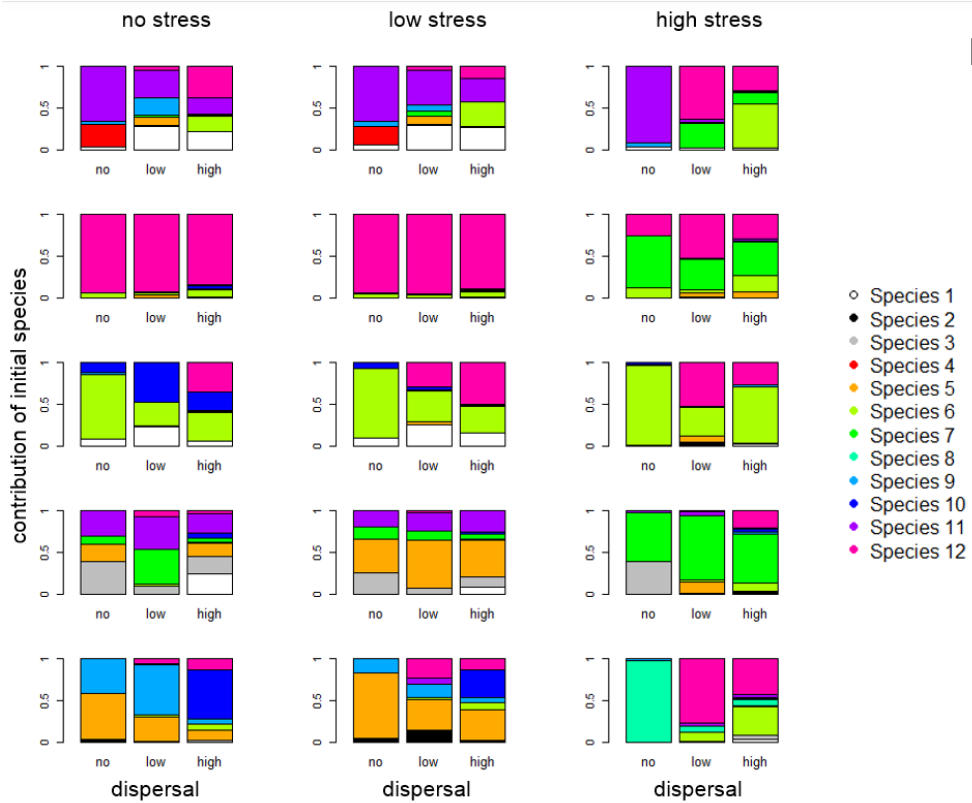


Fig. A1.2. Relative abundance of all species categorized according to initial composition for the three stress and dispersal levels.

Appendix A2. Model validation of statistical results

Contribution of initial species to final biovolume

We used a binomial function to assess the effects of stress and high dispersal (Eq. A2.1).

$$E[Ab_k] = \beta + \sum_{i \in \{low, high\}} \beta_{s,i} stress + \sum_{j=high} \beta_{d,j} dispersal + \sum_{i \in \{low, high\}} \sum_{j=high} \beta_{s,i,d,j} stress \times dispersal + b_k \quad (\text{Eq. A2.1})$$

With Ab_k the abundance of the initial species at the end of the experiment for composition k.

β , $\beta_{s,i}$, $\beta_{d,j}$ and $\beta_{s,i,d,j}$ are the fixed intercept, the estimated effects for stress level j, dispersal level i, and their interaction, respectively. b_k is the random intercept for composition k.

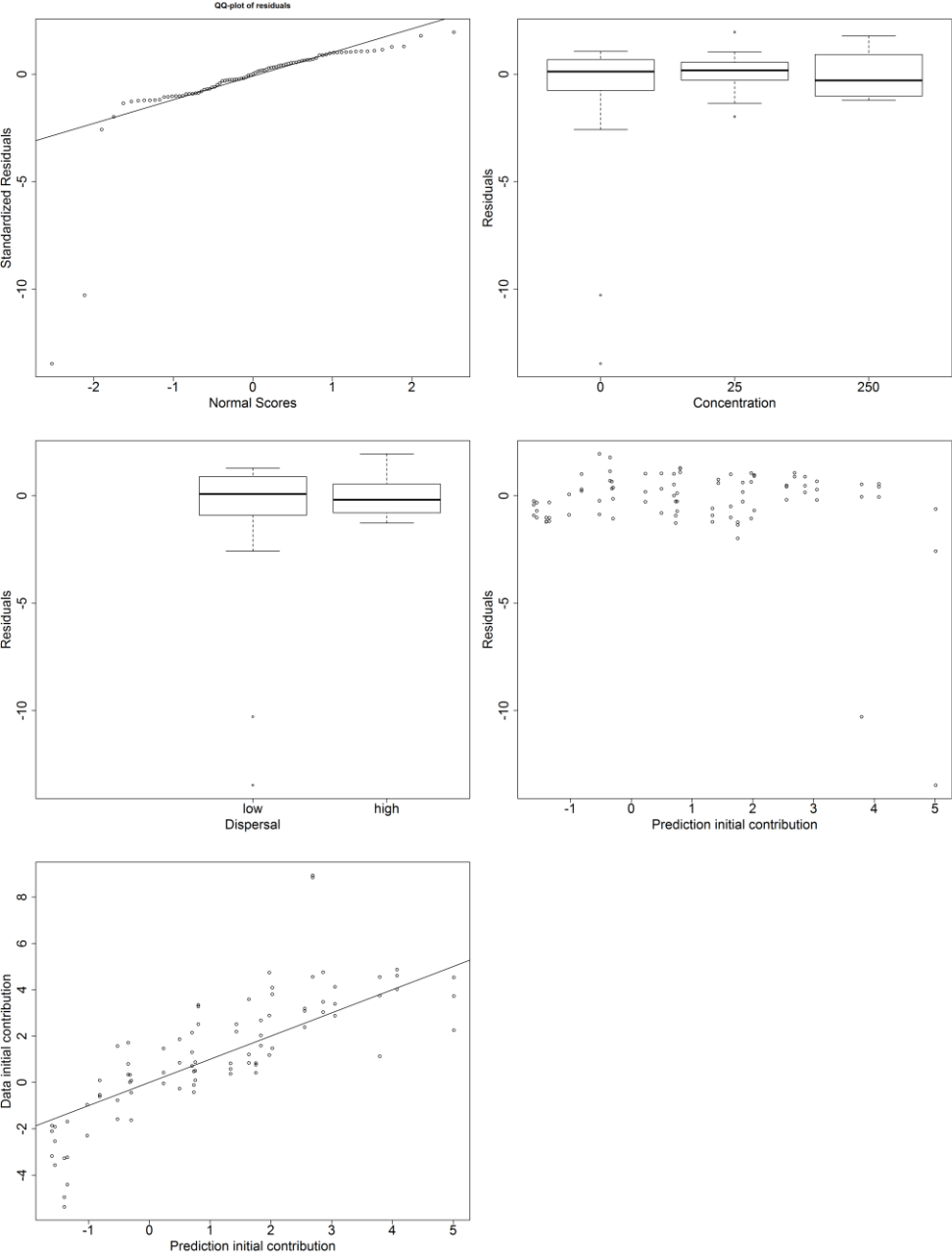


Fig. A2.1 Model validation of contribution of initial species to final biovolume.

Biovolume

$$\begin{aligned}
E[Biov] = & \beta + \beta_t \text{time} + \beta_{t2} \text{time}^2 + \sum_{i \in \{low, high\}} \beta_{s,i} \text{stress} + \\
& \sum_{j \in \{low, high\}} \beta_{d,j} \text{dispersal} + \sum_{i \in \{low, high\}} \beta_{t,s,i} \text{time} \times \text{stress} + \\
& + \sum_{i \in \{low, high\}} \beta_{t2,s,i} \text{time}^2 \times \text{stress} + \sum_{j \in \{low, high\}} \beta_{t,d,j} \text{time} \times \\
& \text{dispersal} + \sum_{i \in \{low, high\}} \sum_{j \in \{low, high\}} \beta_{s,i,d,j} \text{stress} \times \\
& \text{dispersal} + \sum_{i \in \{low, high\}} \sum_{j \in \{low, high\}} \beta_{t,s,i,d,j} \text{time} \times \text{stress} \times \text{dispersal}
\end{aligned} \tag{Eq. A2.2}$$

$E[Biov]$ is the predicted log biovolume. $\beta, \beta_t, \beta_{t2}, \beta_{s,i}, \beta_{d,j}, \beta_{t,s,i}, \beta_{t2,s,i}, \beta_{t,d,j}, \beta_{s,i,d,j}, \beta_{t,s,i,d,j}$ are the estimated fixed intercept and the estimated effects for time, time square, stress level i, dispersal level j, and their interaction respectively.

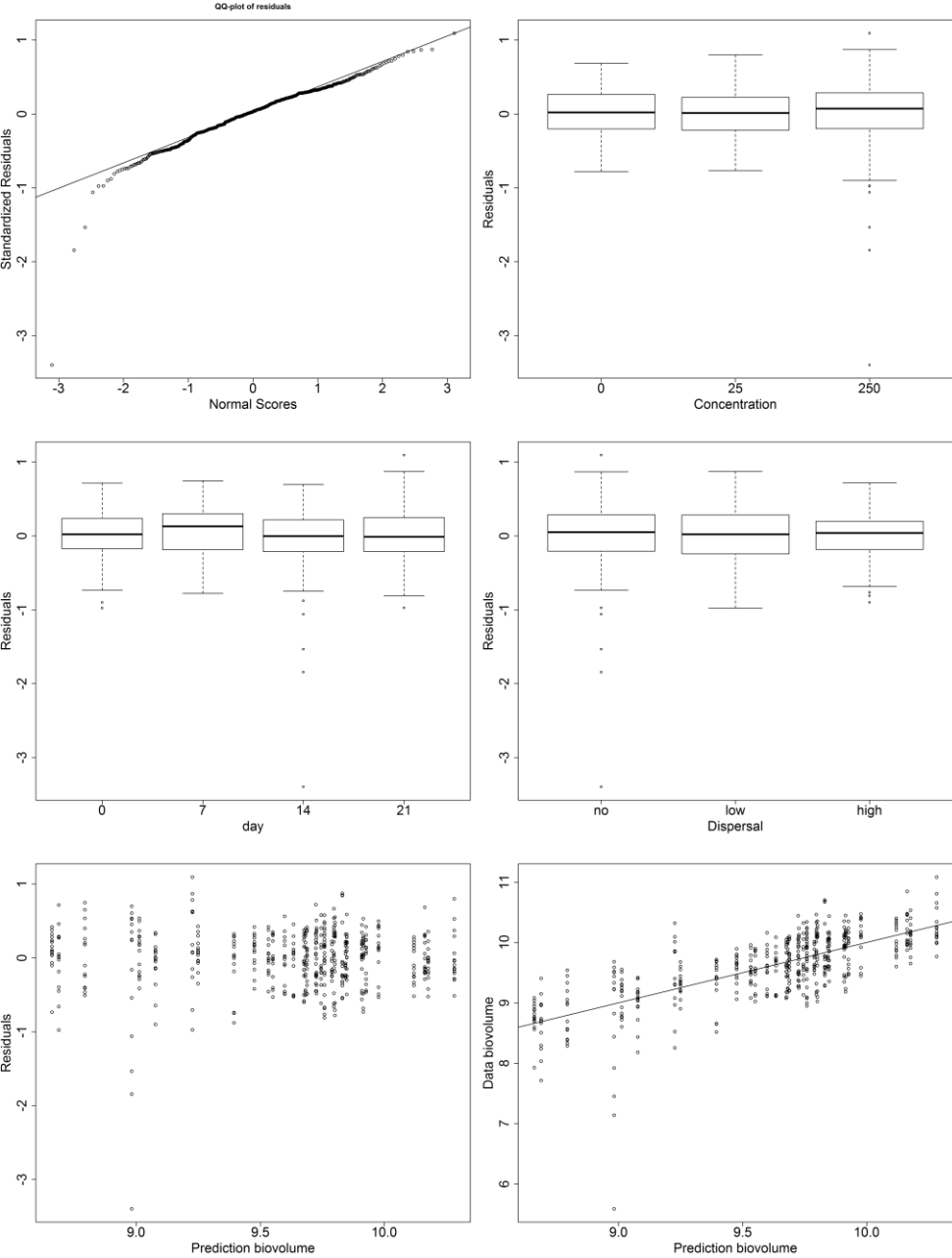


Fig. A2.2. Model validation of biovolume.

Evenness

$$\begin{aligned}
 E[Ev_k] = & \beta + \beta_t \text{time} + \sum_{i \in \{low, high\}} \beta_{s,i} \text{stress} + \sum_{j \in \{low, high\}} \beta_{d,j} \text{dispersal} \\
 & + \sum_{i \in \{low, high\}} \sum_{j \in \{low, high\}} \beta_{s,i,d,j} \text{stress} \times \text{dispersal}
 \end{aligned}
 \tag{Eq. A2.3}$$

$E[Ev]$ is the predicted evenness. β , $\beta_{s,i}$, $\beta_{d,i}$ and $\beta_{s,i,d,j}$ are the estimated fixed intercept and the estimated effects for stress level i , dispersal level j , time and their interaction respectively.

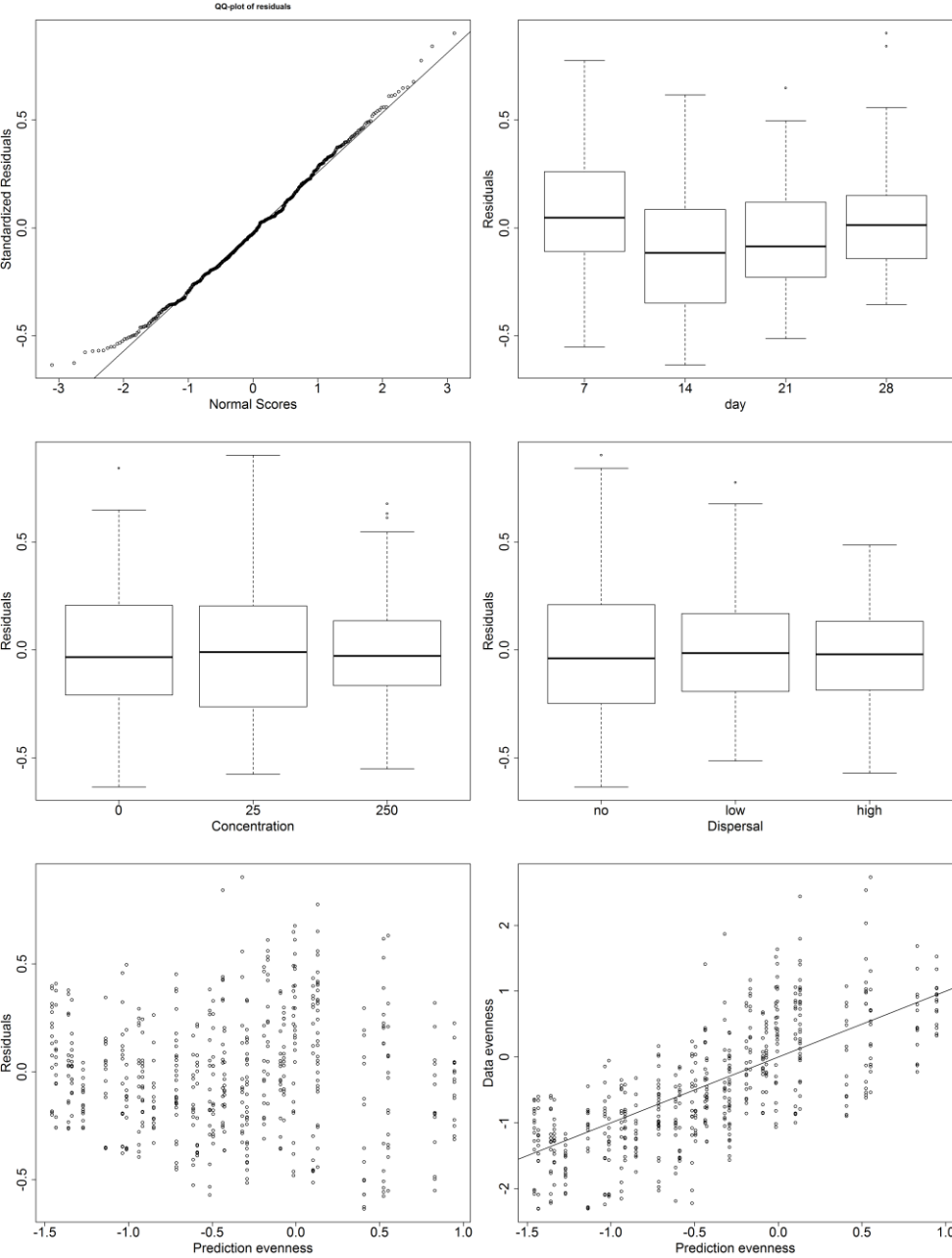


Fig. A2.3. Model validation of evenness.

Relative abundances

$$\begin{aligned}
E[rel_k] = & \beta + \sum_{i \in \{low, high\}} \beta_{s,i} stress + \sum_{j=high} \beta_{d,j} dispersal + \\
& \beta_{Dol} \sqrt{Dol} + \sum_{i \in \{low, high\}} \sum_{j=high} \beta_{s,i,d,j} stress \times dispersal + \quad (Eq. A2.4) \\
& \sum_{i \in \{low, high\}} \beta_{s,i,Dol} stress \times \sqrt{Dol} + \sum_{j=high} \beta_{Dol,j,t} dispersal \times \sqrt{Dol} + \beta_k
\end{aligned}$$

$E[rel_k]$ is the predicted relative abundance of a species in community k with β , $\beta_{s,i}$, $\beta_{s,i}$, β_{Dol} , $\beta_{s,i,d,i}$, $\beta_{s,i,d,j}$, $\beta_{s,i,Dol}$, $\beta_{Dol,j,t}$ the estimated intercept and the estimated effects for stress level i, dispersal level j, day of introduction and their interactions, respectively. Dol is day of introduction.

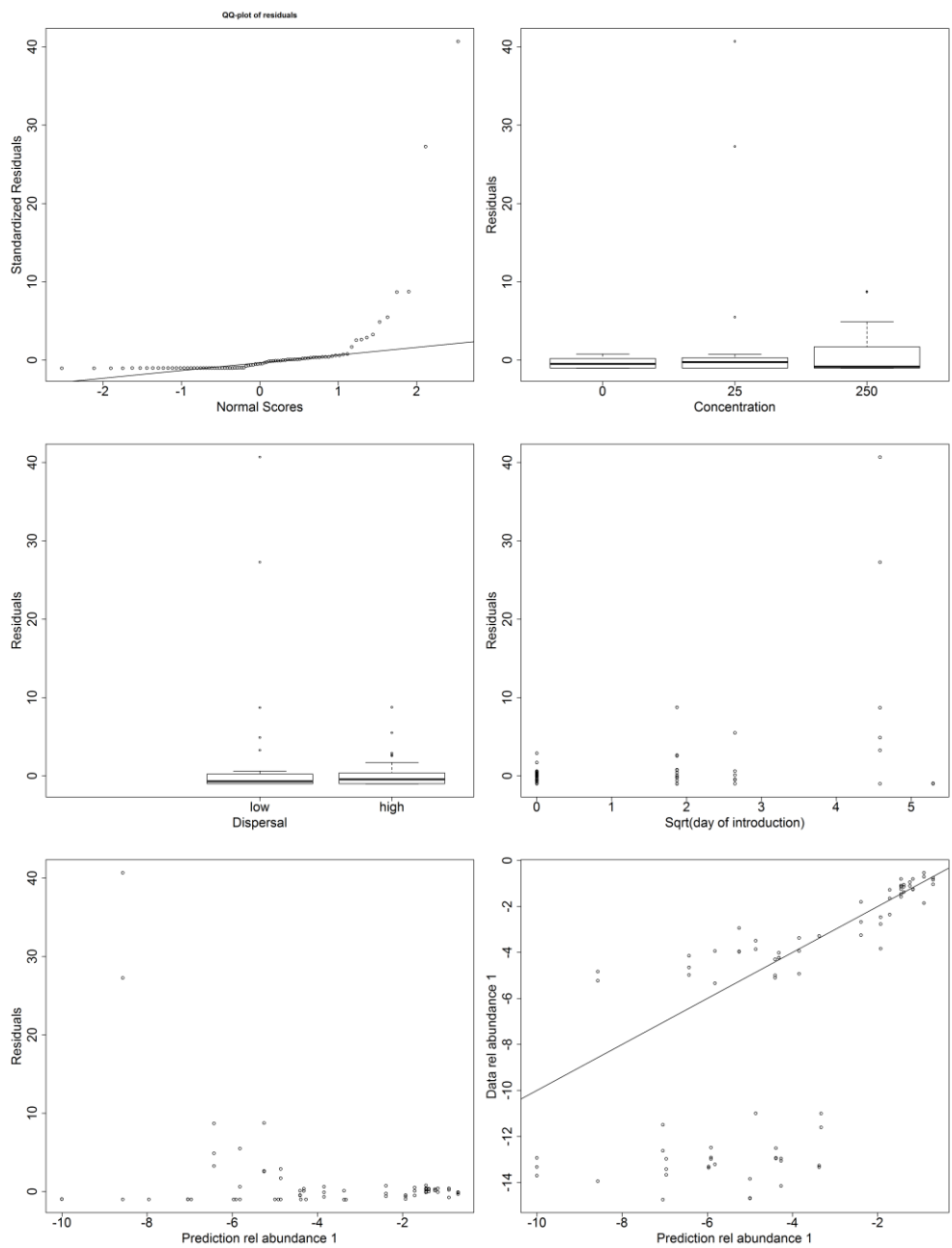


Fig. A2.4. Model validation of species 1.

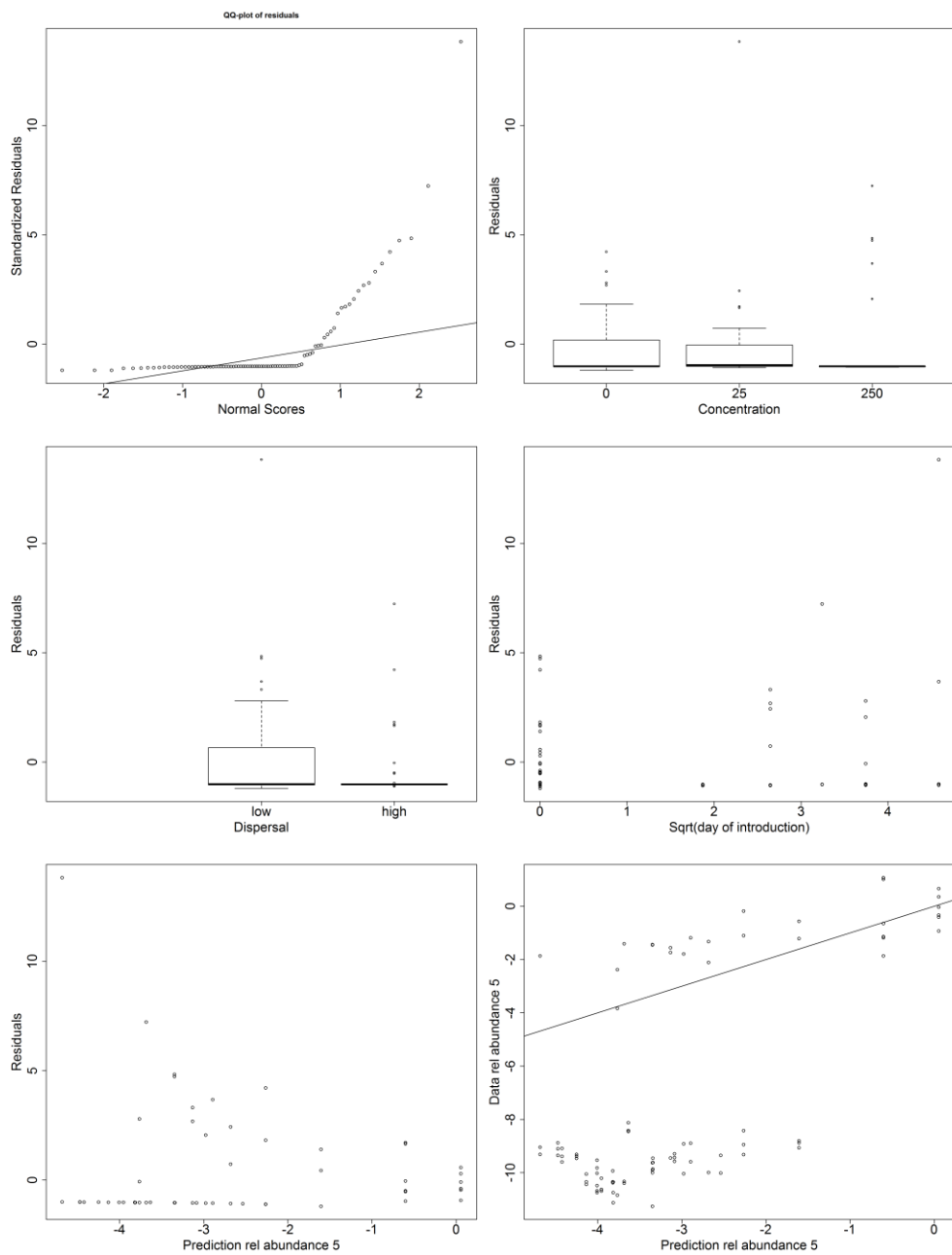


Fig. A2.5. Model validation of Species 5.

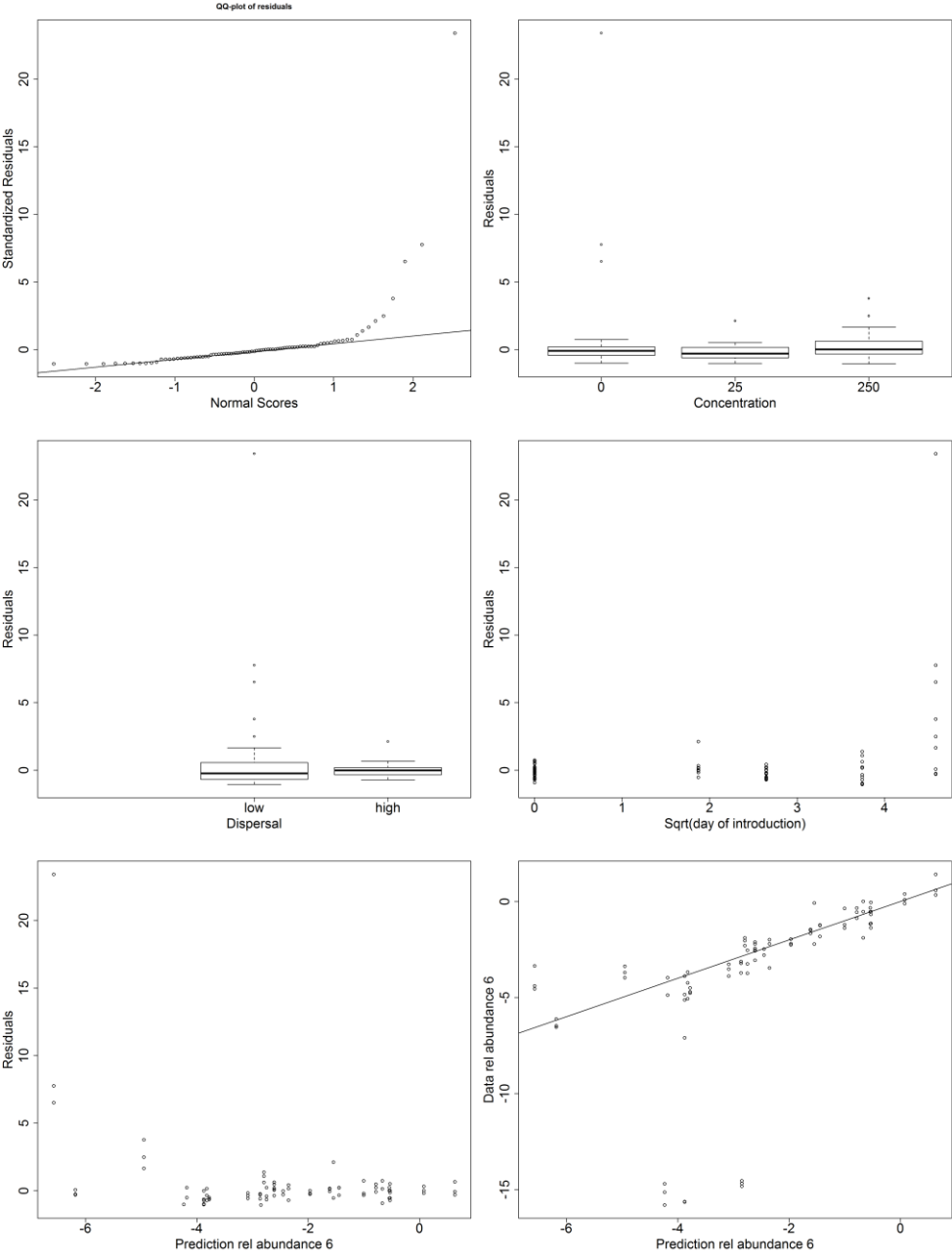


Fig. A2.6. Model validation of species 6.

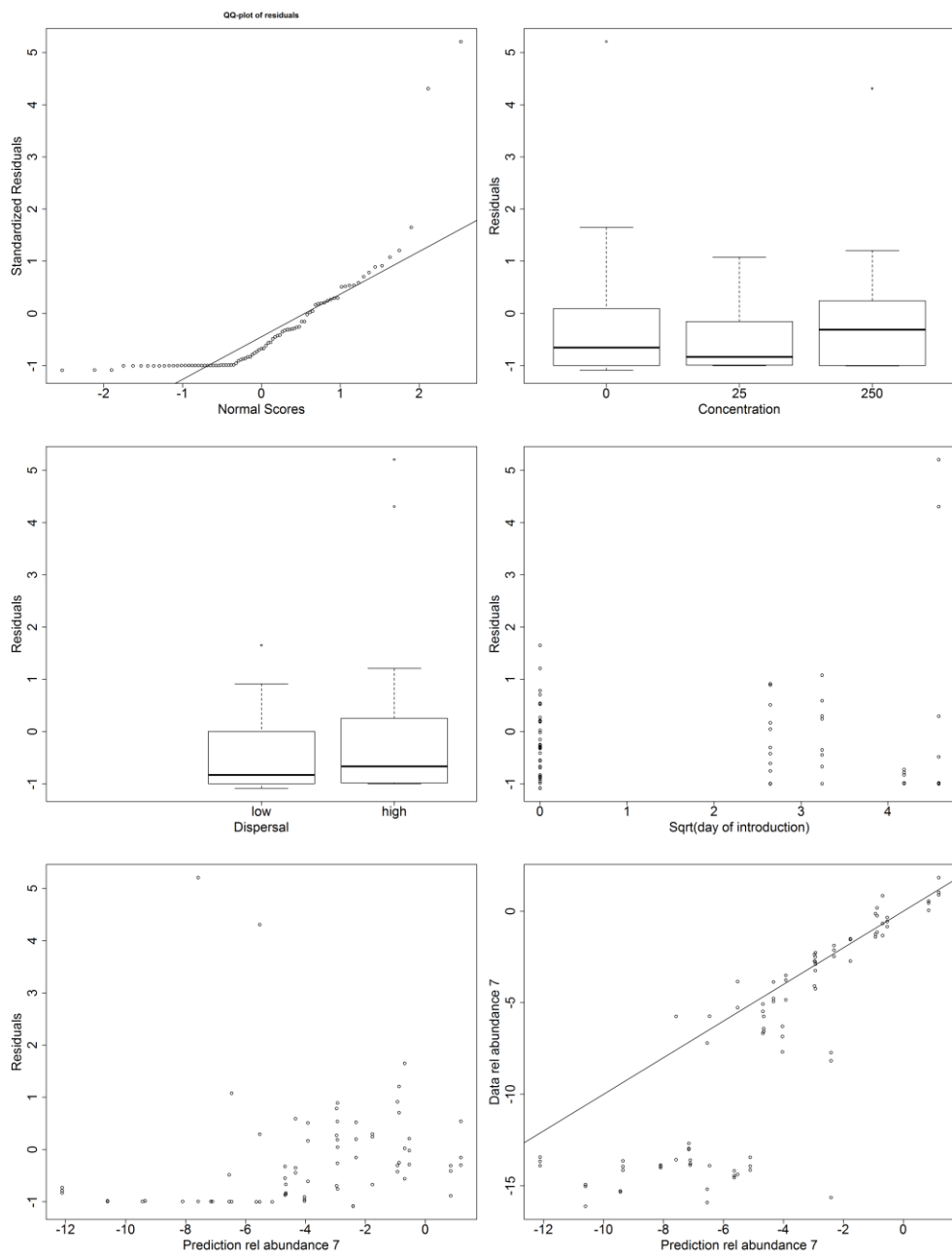


Fig. A2.7. Model validation of species 7.

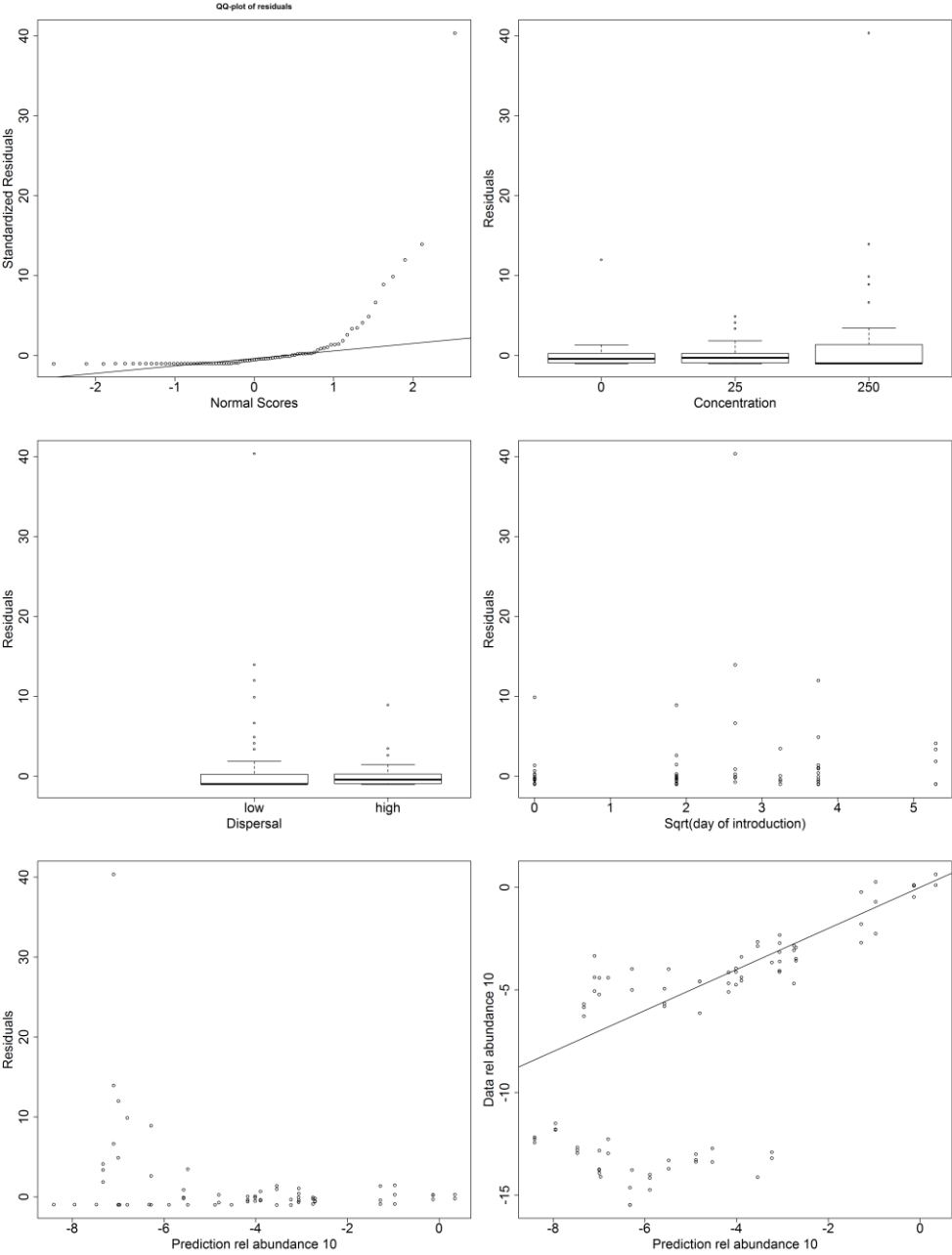


Fig. A2.8. Model validation of species 10.

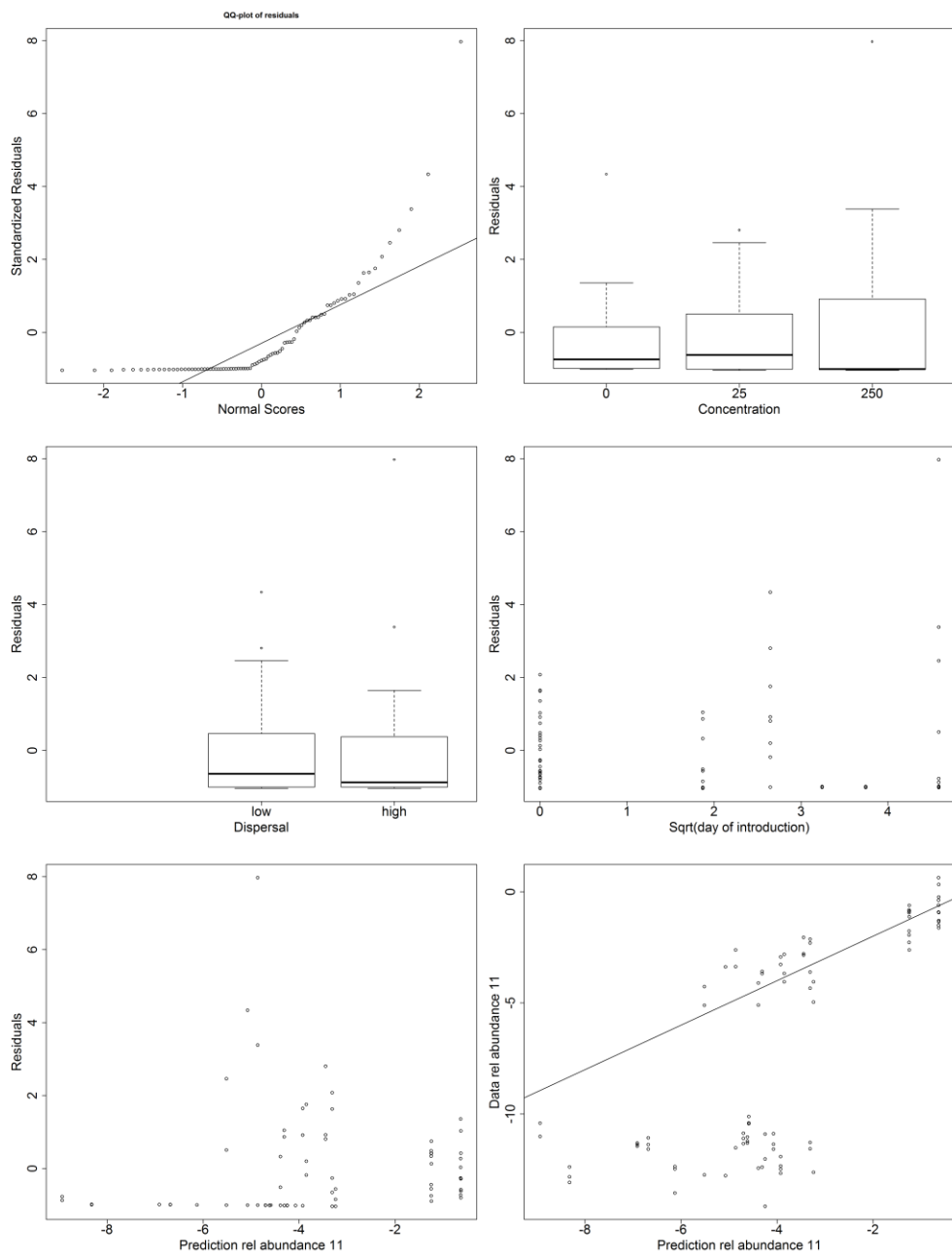


Fig. A2.9. Model validation of species 11.

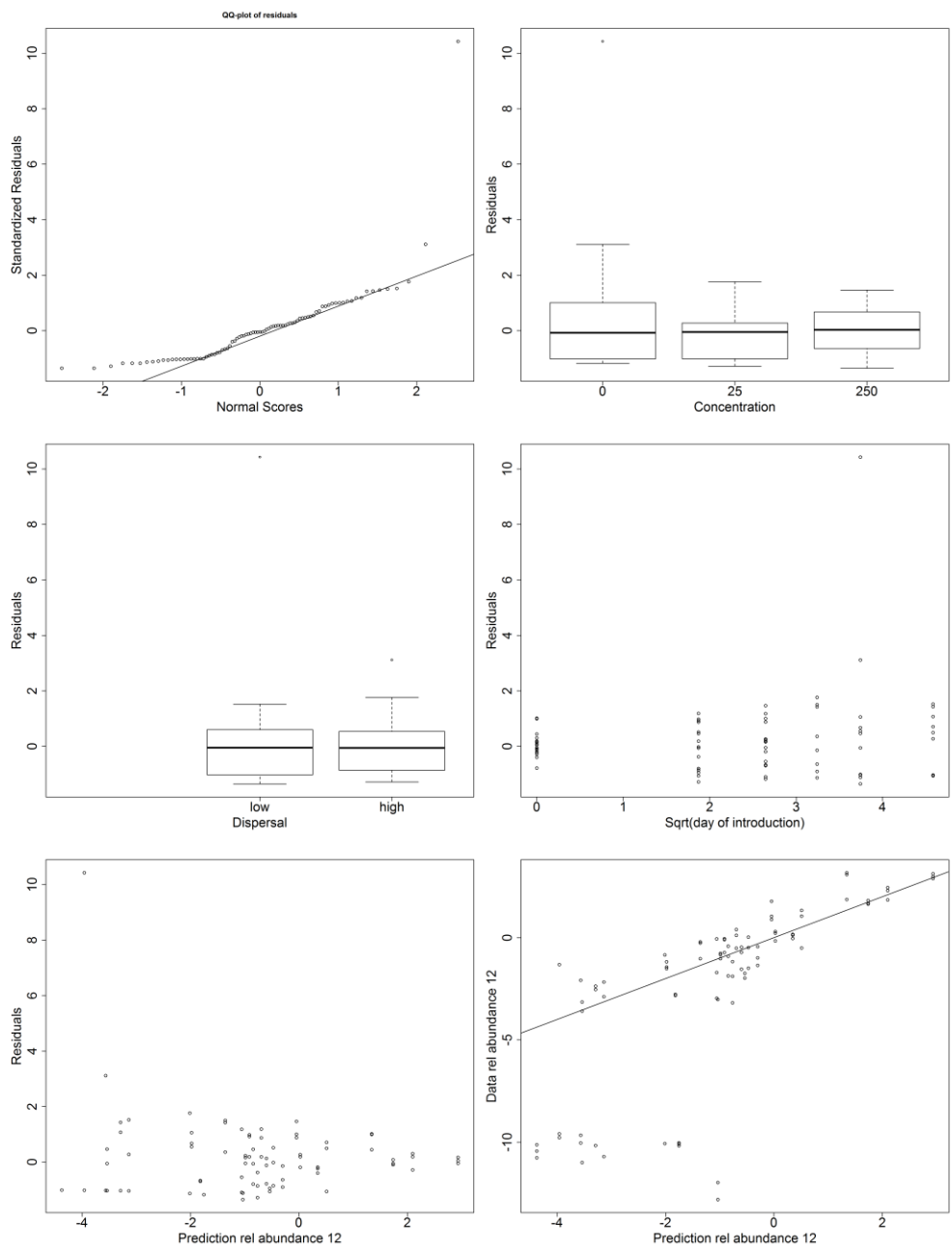


Fig. A2.10. Model validation of species 12.

B

Supporting information for chapter 3

Appendix B1. Model equations

The master equation of the model is given by the following equation:

$$\begin{aligned}
 & \frac{\partial P(N_{1,1}, \dots, N_{n,1}, N_{1,2}, \dots, N_{n,2}, t)}{\partial t} = \\
 & \begin{aligned}
 & \text{Increase local} \left\{ \begin{aligned}
 & T_{1,1}^{l+} P(N_{1,1} - 1, \dots, N_{n,1}, N_{1,2}, \dots, N_{n,2}, t) + \dots \\
 & + T_{n,1}^{l+} P(N_{1,1}, \dots, N_{n,1} - 1, N_{1,2}, \dots, N_{n,2}, t) + \\
 & T_{1,2}^{l+} P(N_{1,1}, \dots, N_{n,1}, N_{1,2} - 1, \dots, N_{n,2}, t) + \dots \\
 & + T_{n,2}^{l+} P(N_{1,1}, \dots, N_{n,1}, N_{1,2}, \dots, N_{n,2} - 1, t) +
 \end{aligned} \right. \\
 & \text{Decrease local} \left\{ \begin{aligned}
 & T_{1,1}^{l-} P(N_{1,1} + 1, \dots, N_{n,1}, N_{1,2}, \dots, N_{n,2}, t) + \dots \\
 & + T_{n,1}^{l-} P(N_{1,1}, \dots, N_{n,1} + 1, N_{1,2}, \dots, N_{n,2}, t) + \\
 & T_{1,2}^{l-} P(N_{1,1}, \dots, N_{n,1}, N_{1,2} + 1, \dots, N_{n,2}, t) + \dots \\
 & + T_{n,2}^{l-} P(N_{1,1}, \dots, N_{n,1}, N_{1,2}, \dots, N_{n,2} + 1, t) +
 \end{aligned} \right. \quad (\text{Eq. B1.1}) \\
 & \text{Dispersal} \left\{ \begin{aligned}
 & T_{1,1}^{r+} P(N_{1,1} - 1, \dots, N_{n,1}, N_{1,2} + 1, \dots, N_{n,2}, t) + \dots \\
 & + T_{n,1}^{r+} P(N_{1,1}, \dots, N_{n,1} - 1, N_{1,2}, \dots, N_{n,2}, t) + \\
 & T_{2,1}^{r+} P(N_{1,1} + 1, \dots, N_{n,1}, N_{1,2} - 1, \dots, N_{n,2}, t) + \dots \\
 & + T_{n,2}^{r+} P(N_{1,1} + 1, \dots, N_{n,1}, N_{1,2}, \dots, N_{n,2} - 1, t) - \\
 & (T_{1,1}^{l+} + \dots + T_{n,1}^{l+} + T_{1,2}^{l+} + \dots + T_{n,2}^{l+} + T_{1,1}^{l-} + \dots + T_{n,1}^{l-} + T_{1,2}^{l-} + \dots + \\
 & T_{n,2}^{l-} + T_{1,1}^{r+} + \dots + T_{n,1}^{r+} + T_{2,1}^{r+} + \dots + \\
 & T_{N_{n,2}}^{r+}) P(N_{1,1}, \dots, N_{n,1}, N_{1,2}, \dots, N_{n,2}, t)
 \end{aligned} \right.
 \end{aligned}
 \end{aligned}$$

where $P(N_{1,1}, \dots, N_{n,1}, N_{1,2}, \dots, N_{n,2}, t)$ is the probability that there are $N_{i,j}$ individuals of species i , with $i \in \{1, \dots, n\}$ in community j , with $j \in \{1, 2\}$ at time t , and T is the transition rate of the population from one state to its neighboring state. The subscript of T refers to the species whose density changes, and the superscript denotes whether its density increases by one or decreases by one and if this process is due to a local (l) or regional (r) process. The transition rates are given by Eq. 3.1-3.4.

When $d_{i,j} = d_i$, $a_{i,k,j} = a_{i,k}$ and $m_{i,j} = m$, then the ordinary differential equation is given by:

$$\frac{dN_{i,1}}{dt} = N_{i,1} \left(b_{i,1} - d_i - \sum_{k=1}^n a_{i,k} N_{k,1} \right) + mN_{i,2} - mN_{i,1} \quad (\text{Eq. B1.2})$$

$$\frac{dN_{i,2}}{dt} = N_{i,2} \left(b_{i,2} - d_i - \sum_{k=1}^n a_{i,k} N_{k,2} \right) + mN_{i,1} - mN_{i,2} \quad (\text{Eq. B1.3})$$

Appendix B2. Model validation

Table B2.1. Parameter values used for Fig. B1.1.

Parameter	Name	Community 1	Community 2
m	Dispersal rate	0.5	0.5
N_0	Initial abundance	10	10
a	Interaction coefficient	0.001	0.002
b	Birth rate	0.5	0.5
d	Death rate	0.1	0.1

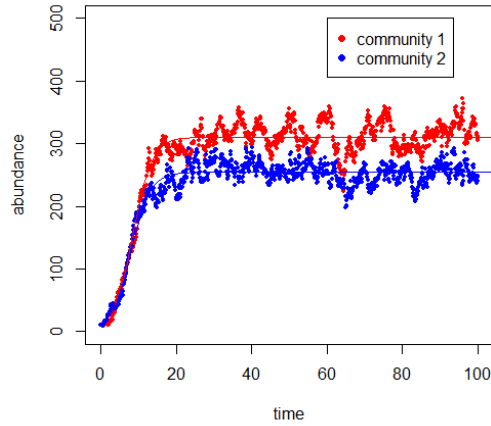


Fig. B2.1. Abundance of 1 species in 2 connected communities in function of time. Dots: stochastic model, lines: dynamic Lotka-Volterra model. Parameter values, see table B1.1.

Table B2.2. Parameter values used for Fig. B1.2.

Parameter	Name	Community 1	Community 2
m	Dispersal rate	0.5	0.5
N_0	Initial abundance	100	100
a	Interaction coefficient	0	0
b	Birth rate	0	0
d	Death rate	0	0

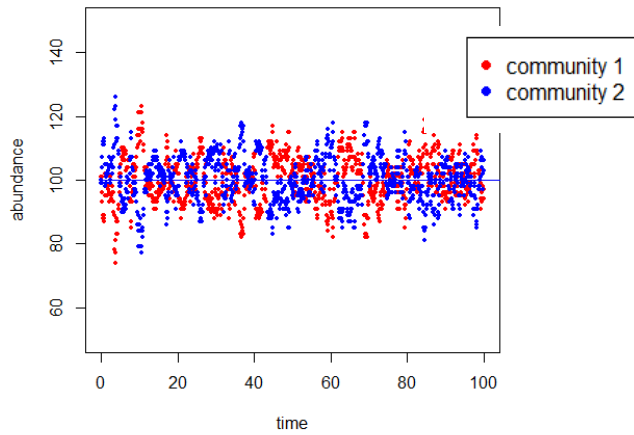


Fig. B2.2. Abundance of 1 species in 2 connected communities in function of time. Dots: stochastic model, lines: dynamic Lotka-Volterra model. Parameter values, see table B1.2.

Table B2.3. Parameter values used for Fig. B1.3.

Parameter	Name	Community 1	Community 2
m	Dispersal rate	0	0
N_0	Initial abundance	100	100
a	Interaction coefficient	Table 3.1	Table 3.1
b	Birth rate	Table 3.1	Table 3.1
d	Death rate	Table 3.1	Table 3.1

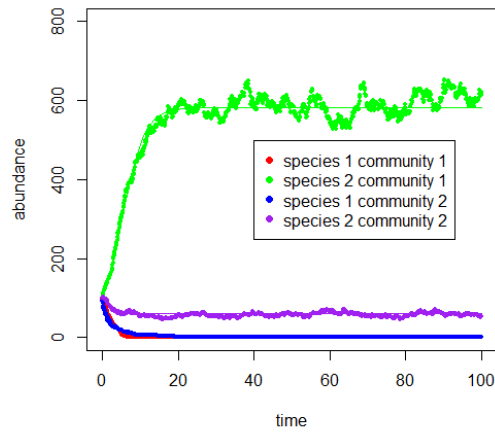


Fig. B2.3. Abundance of 2 species in 2 connected communities in function of time. Dots: stochastic model, lines: dynamic Lotka-Volterra model. Parameter values, see table B1.3.

Table B2.4. Parameter values used for Fig. B1.4.

Parameter	Name	Community 1	Community 2
m	Dispersal rate	0.2	0.2
N_0	Initial abundance	100	100
a	Interaction coefficient	0	0
b	Birth rate	0	0
d	Death rate	0	0

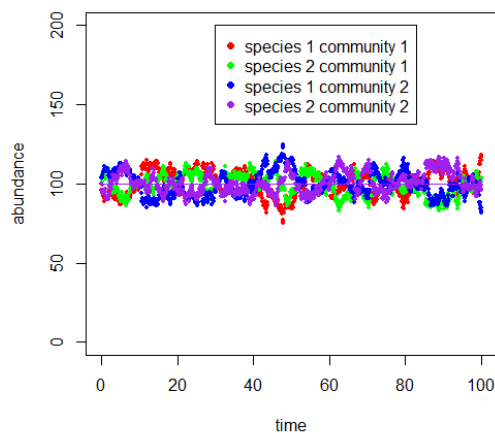


Fig. B2.4. Abundance of 2 species in 2 connected communities in function of time. Dots: stochastic model, lines: dynamic Lotka-Volterra model. Parameter values, see table B1.4.

Appendix B3. Figures

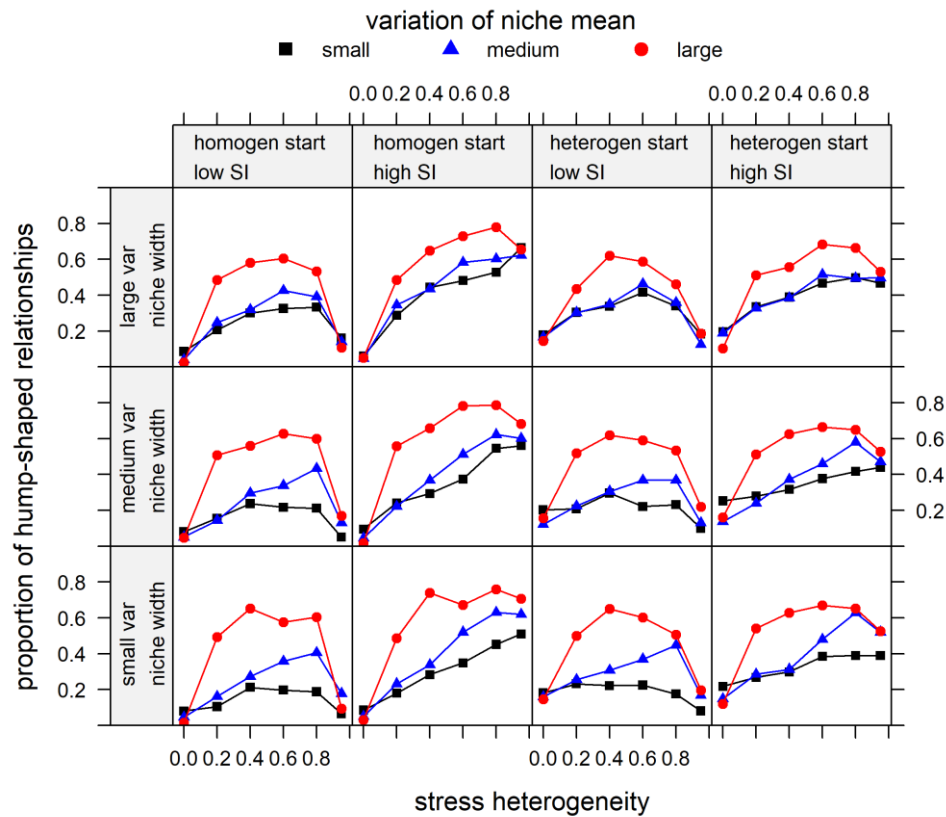


Fig. B3.1. Proportion of hump-shaped relationships in function of the stress-intensity gradient when the threshold value between minimum and maximum diversity is 0.1. A reduction of the threshold value from 1 to 0.1 did not substantially change the results. Relationships without convergence are removed from the analysis. Abbreviations: homogen init/heterogen init: homogeneous or heterogeneous initial community composition; small SI/high SI: low-stressed and high-stressed community; var: variation.

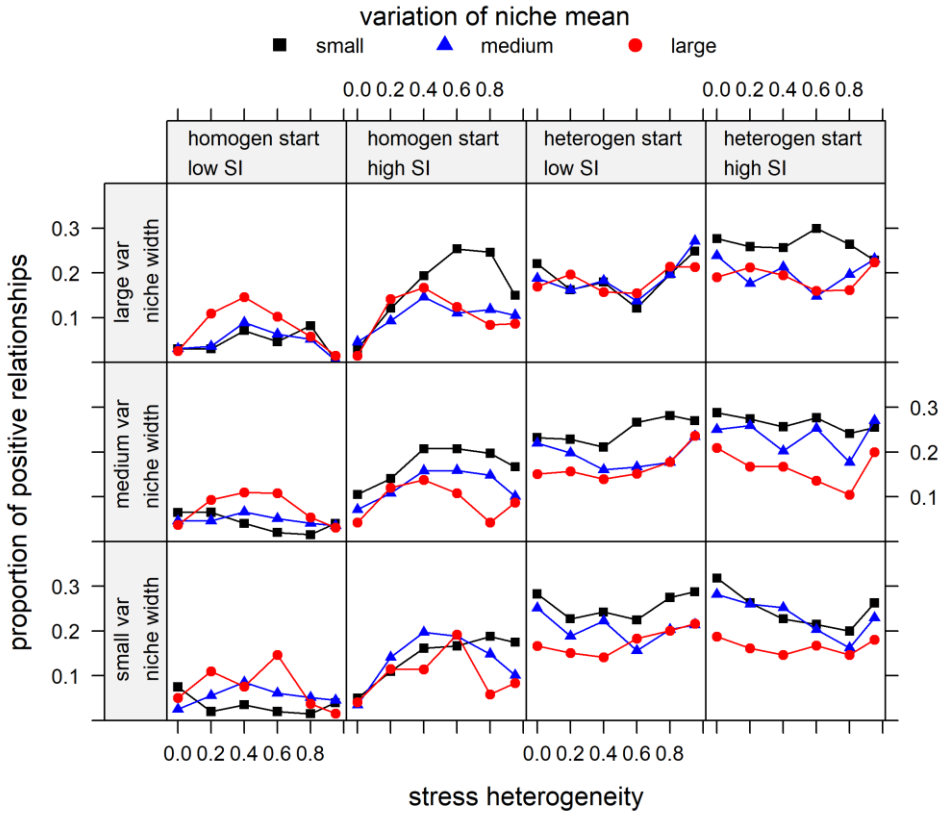


Fig. B3.2. Proportion of positive relationships in function of the stress-intensity gradient when the threshold value between minimum and maximum diversity is 0.1. A reduction of the threshold value from 1 to 0.1 did not substantially change the results. Relationships without convergence are removed from the analysis. Abbreviations: homogen init/heterogen init: homogeneous or heterogeneous initial community composition; small SI/high SI: low-stressed and high-stressed community; var: variation.

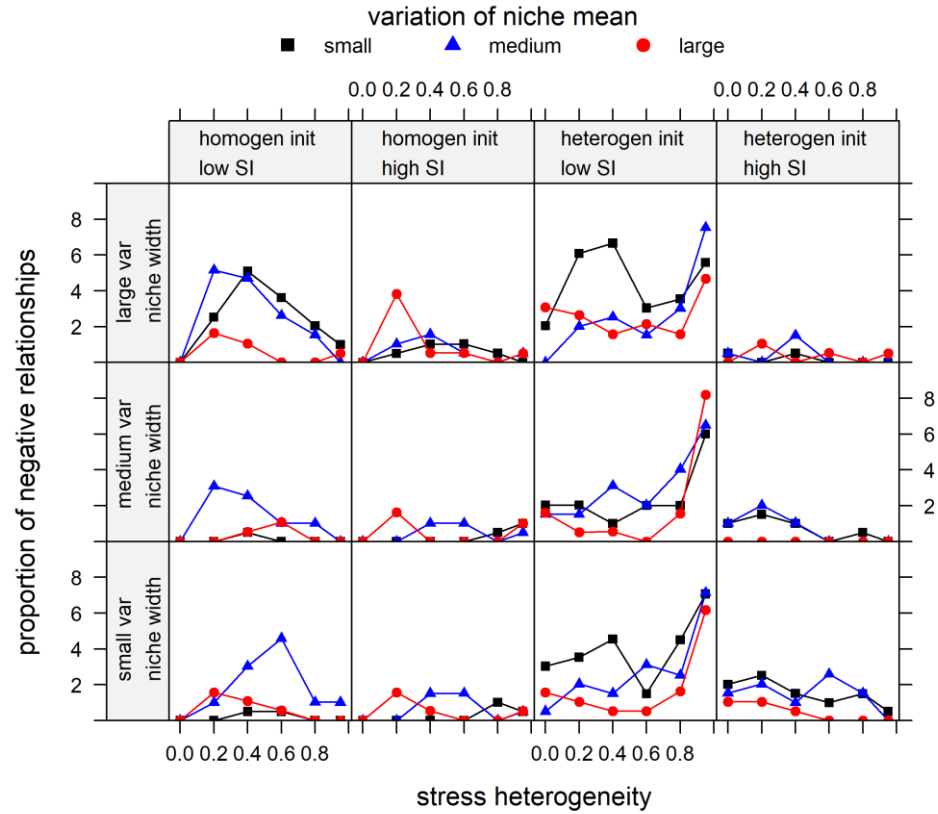


Fig. B3.3. Proportion of negative relationships in function of the stress-intensity gradient. Relationships without convergence are removed from the analysis. Abbreviations: homogen init/heterogen init: homogeneous or heterogeneous initial community composition; small SI/high SI: low-stressed and high-stressed community; var: variation.

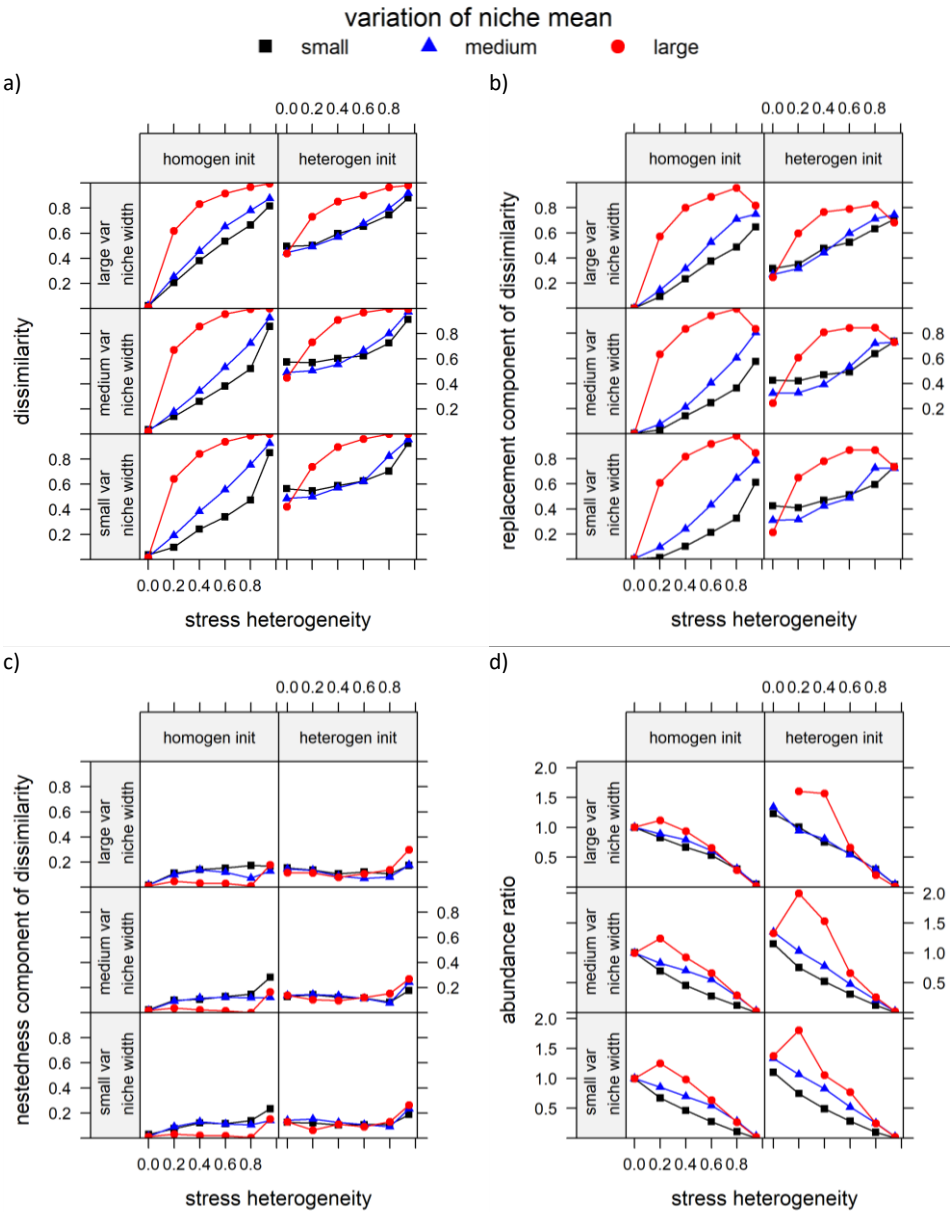


Fig. B3.4. a) The average Sørensen dissimilarity index between the low-stressed and high-stressed community at the lowest dispersal rate over all iterations. b) The replacement component of the Sørensen dissimilarity index. c) The nestedness component of the Sørensen dissimilarity index. d) the mean log abundance ratio between the high-stressed and low-stressed community over all iterations. Abbreviations: homogen init/heterogen init: homogeneous or heterogeneous initial community composition; var: variation.

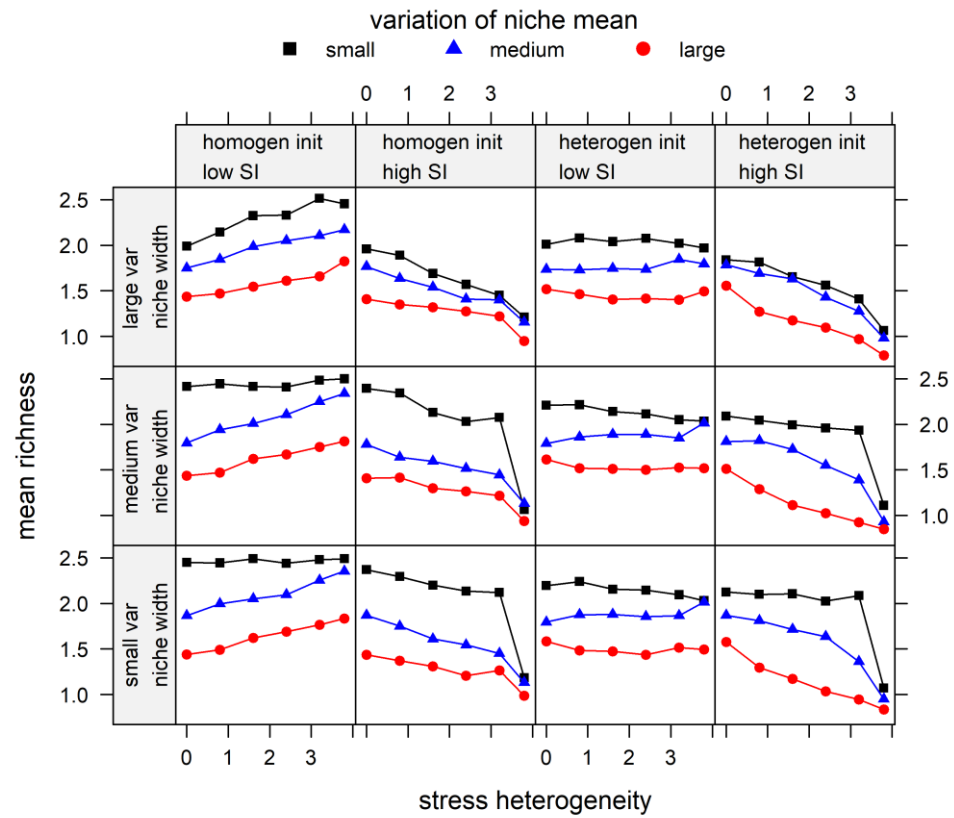


Fig. B3.5. Average local richness over all iterations in function of stress heterogeneity at the lowest dispersal rate. Abbreviations: homogen init/heterogen init: homogeneous or heterogeneous initial community composition; small SI/high SI: low-stressed and high-stressed community; var: variation.

C

Supporting information for chapter 4

Table C1. Algae strains with their respective volume, mean growth rate μ , mean carrying capacity K , EC_{50} and slope (s) for the growth rate and carrying capacity. Mean growth rate and mean carrying capacity were determined by using a logistic growth curve. EC_{50} and s are the turning point and slope of the log-logistic dose-response relationship (eq. 4).

Genus name	Volume (μm^3)	Growth rate at 0 $\mu g\ l^{-1}$ (d^{-1})	Carrying capacity at 0 $\mu g\ l^{-1}$ (μm^3)	$EC_{50,\mu}$ ($\mu g\ l^{-1}$)	s_μ	$EC_{50,K}$ ($\mu g\ l^{-1}$)	s_K
<i>Thalassiosira</i>	27784	0.35	5.1×10^8	95	16.7	74	55.4
<i>Odontella</i>	72804	0.70	3.2×10^9	480	13.8	88	16.6
<i>Melosira</i>	24980	0.75	2.4×10^8	137	1.0	209	15.2
<i>Asterionella</i>	1116	0.81	1.8×10^8	64	2.2	85	18.2
<i>Navicula</i>	563	0.84	2.2×10^7	121	1.5	102	14.9
<i>Asterionellopsis</i>	482	0.99	1.6×10^8	53	0.7	192	14.5

Table C2a. The concentration (conc) of atrazine in the added medium, theoretical concentration of atrazine in the community after medium renewal and measured concentration of atrazine in the unstressed and stressed community at a low stressor flux.

Date (day)	Conc to add in unstressed ($\mu g\ l^{-1}$)	Conc to add in stressed ($\mu g\ l^{-1}$)	Conc unstressed ($\mu g\ l^{-1}$)	Conc stressed ($\mu g\ l^{-1}$)	Measured conc unstressed ($\mu g\ l^{-1}$)	Measured conc stressed ($\mu g\ l^{-1}$)
4	38	213	13	238		
8	46	204	24	226		
12	54	196	34	216		
16	61	189	43	207		
20	68	182	51	199	46	220

Table C2b. The concentration (conc) of atrazine in the added medium, theoretical concentration of atrazine in the community after medium renewal and measured concentration of atrazine in the unstressed and stressed community at a medium stressor flux.

Date (day)	Conc to add in unstressed ($\mu g\ l^{-1}$)	Conc to add in stressed ($\mu g\ l^{-1}$)	Conc unstressed ($\mu g\ l^{-1}$)	Conc stressed ($\mu g\ l^{-1}$)	Measured conc unstressed ($\mu g\ l^{-1}$)	Measured conc stressed ($\mu g\ l^{-1}$)
4	75	175	25	225		
8	85	165	45	205		
12	93	157	61	189		
16	99	151	74	176		
20	105	145	84	166	71	174

Table C2c. The concentration (conc) of atrazine in the added medium, theoretical concentration of atrazine in the community after medium renewal and measured concentration of atrazine in the unstressed and stressed community at a high stressor flux.

Time (day)	Conc to add in unstressed ($\mu\text{g l}^{-1}$)	Conc to add in stressed ($\mu\text{g l}^{-1}$)	Conc unstressed ($\mu\text{g l}^{-1}$)	Conc stressed ($\mu\text{g l}^{-1}$)	Measured conc unstressed ($\mu\text{g l}^{-1}$)	Measured conc stressed ($\mu\text{g l}^{-1}$)
4	113	138	38	213		
8	116	134	64	186		
12	119	131	82	168		
16	121	129	95	155		
20	122	128	104	146	86	151

Table C3. Nutrient concentrations. rep: replicate, ns: unstressed, s: stressed, NA: not measured.

time (d)	Environ- mental flux	disper sal	commu nity	re p	Nitrate-N ($mg\ l^{-1}$)	Silicate-Si ($mg\ l^{-1}$)	Phosphate-P ($mg\ l^{-1}$)
8	0	0	ns	1	7.8958	1.0774	NA
8	0	0.05	ns	1	7.229	1.5498	NA
8	0	0.1	ns	1	6.9406	1.5069	NA
8	0	0.15	ns	1	7.3994	0.8437	NA
8	0	0.2	ns	1	6.9607	0.6401	NA
8	0.05	0	ns	1	7.01	14.5686	NA
8	0.05	0.05	ns	1	6.601	1.6588	NA
8	0.05	0.1	ns	1	6.8595	0.939	NA
8	0.05	0.15	ns	1	6.0714	1.5444	NA
8	0.05	0.2	ns	1	7.2589	0.8918	NA
8	0.1	0	ns	1	7.6041	1.0654	NA
8	0.1	0.05	ns	1	7.3086	0.5366	NA
8	0.1	0.1	ns	1	7.6359	1.1502	NA
8	0.1	0.15	ns	1	7.3346	0.7612	NA
8	0.1	0.2	ns	1	7.76	1.4583	NA
8	0.15	0	ns	1	7.6298	0.2043	NA
8	0.15	0.05	ns	1	7.1377	1.6047	NA
8	0.15	0.1	ns	1	5.7851	0.0835	NA
8	0.15	0.15	ns	1	8.9798	0.6369	NA
8	0.15	0.2	ns	1	7.8581	0.5435	NA
8	0	0	ns	2	NA	NA	0.1814
8	0	0.05	ns	2	NA	NA	0.1718
8	0	0.1	ns	2	NA	NA	0.2112
8	0	0.15	ns	2	NA	NA	0.1864
8	0	0.2	ns	2	NA	NA	0.1763
8	0.05	0	ns	2	NA	NA	0.2249
8	0.05	0.05	ns	2	NA	NA	0.1455
8	0.05	0.1	ns	2	NA	NA	0.1708
8	0.05	0.15	ns	2	NA	NA	0.1329
8	0.05	0.2	ns	2	NA	NA	0.0905
8	0.1	0	ns	2	NA	NA	0.1966
8	0.1	0.05	ns	2	NA	NA	0.2345
8	0.1	0.1	ns	2	NA	NA	0.1742
8	0.1	0.15	ns	2	NA	NA	0.2062
8	0.1	0.2	ns	2	NA	NA	0.1556
8	0.15	0	ns	2	NA	NA	0.1339
8	0.15	0.05	ns	2	NA	NA	0.1733
8	0.15	0.1	ns	2	NA	NA	0.0582
8	0.15	0.15	ns	2	NA	NA	0.1779
8	0.15	0.2	ns	2	NA	NA	0.0189
16	0	0	ns	2	3.2066	NA	<0.05
16	0	0.05	ns	2	4.1204	NA	0.0653
16	0	0.1	ns	2	3.5374	NA	0.0658
16	0	0.15	ns	2	NA	NA	NA
16	0	0.2	ns	2	NA	NA	NA
16	0.05	0	ns	2	2.26936	NA	<0.05
16	0.05	0.05	ns	2	2.5404	NA	0.0749
16	0.05	0.1	ns	2	2.4126	NA	<0.05
16	0.05	0.15	ns	2	2.4003	NA	<0.05
16	0.05	0.2	ns	2	2.509	NA	0.1031
16	0.1	0	ns	2	2.2605	NA	<0.05
16	0.1	0.05	ns	2	2.2014	NA	<0.05
16	0.1	0.1	ns	2	2.4415	NA	<0.05
16	0.1	0.15	ns	2	2.0004	NA	<0.05

16	0.1	0.2	ns	2	1.9213	NA	<0.05
16	0.15	0	ns	2	2.2535	NA	<0.05
16	0.15	0.05	ns	2	2.7182	NA	0.0567
16	0.15	0.1	ns	2	1.8491	NA	<0.05
16	0.15	0.15	ns	2	1.8509	NA	0.0577
16	0.15	0.2	ns	2	2.0331	NA	0.0648
16	0	0	ns	3	NA	0.302	NA
16	0	0.05	ns	3	NA	0.2748	NA
16	0	0.1	ns	3	NA	0.1917	NA
16	0	0.15	ns	3	NA	NA	NA
16	0	0.2	ns	3	NA	NA	NA
16	0.05	0	ns	3	NA	0.1212	NA
16	0.05	0.05	ns	3	NA	0.2617	NA
16	0.05	0.1	ns	3	NA	0.3543	NA
16	0.05	0.15	ns	3	NA	0.2712	NA
16	0.05	0.2	ns	3	NA	0.0934	NA
16	0.1	0	ns	3	NA	0.2916	NA
16	0.1	0.05	ns	3	NA	0.7589	NA
16	0.1	0.1	ns	3	NA	0.4447	NA
16	0.1	0.15	ns	3	NA	0.3452	NA
16	0.1	0.2	ns	3	NA	0.2048	NA
16	0.15	0	ns	3	NA	<0.1	NA
16	0.15	0.05	ns	3	NA	0.118	NA
16	0.15	0.1	ns	3	NA	0.1841	NA
16	0.15	0.15	ns	3	NA	NA	NA
16	0.15	0.2	ns	3	NA	0.1787	NA
24	0	0	ns	1	0.9516	0.3479	NA
24	0	0.05	ns	1	0.7842	0.2717	NA
24	0	0.1	ns	1	0.9553	0.3048	NA
24	0	0.15	ns	1	0.7196	0.1841	NA
24	0	0.2	ns	1	1.1328	0.1028	NA
24	0.05	0	ns	1	4.0076	0.1728	NA
24	0.05	0.05	ns	1	3.7665	0.3712	NA
24	0.05	0.1	ns	1	2.7859	0.1616	NA
24	0.05	0.15	ns	1	1.8366	0.1512	NA
24	0.05	0.2	ns	1	3.5738	0.3125	NA
24	0.1	0	ns	1	4.2411	0.189	NA
24	0.1	0.05	ns	1	4.971	0.531	NA
24	0.1	0.1	ns	1	4.5919	0.1575	NA
24	0.1	0.15	ns	1	5.1635	NA	NA
24	0.1	0.2	ns	1	5.2576	0.1589	NA
24	0.15	0	ns	1	5.0149	0.1239	NA
24	0.15	0.05	ns	1	2.1148	1.2591	NA
24	0.15	0.1	ns	1	4.9669	<0.1	NA
24	0.15	0.15	ns	1	<0.2	0.9505	NA
24	0.15	0.2	ns	1	0.2354	0.3402	NA
24	0	0	s	1	11.441	>5	NA
24	0	0.05	s	1	11.246	>5	NA
24	0	0.1	s	1	10.259	>5	NA
24	0	0.15	s	1	10.405	>5	NA
24	0	0.2	s	1	10.539	>5	NA
24	0.05	0	s	1	11.206	>5	NA
24	0.05	0.05	s	1	9.8305	>5	NA
24	0.05	0.1	s	1	9.5413	>5	NA
24	0.05	0.15	s	1	9.8979	>5	NA
24	0.05	0.2	s	1	9.1202	>5	NA
24	0.1	0	s	1	10.88	>5	NA
24	0.1	0.05	s	1	9.6177	>5	NA

Appendix C

24	0.1	0.1	s	1	9.22	>5	NA
24	0.1	0.15	s	1	9.495	>5	NA
24	0.1	0.2	s	1	8.8331	>5	NA
24	0.15	0	s	1	10.526	>5	NA
24	0.15	0.05	s	1	9.8427	>5	NA
24	0.15	0.1	s	1	8.5868	>5	NA
24	0.15	0.15	s	1	9.3523	>5	NA
24	0.15	0.2	s	1	9.295	>5	NA
24	0	0	ns	2	NA	NA	<0.05
24	0	0.05	ns	2	NA	NA	<0.05
24	0	0.1	ns	2	NA	NA	<0.05
24	0	0.15	ns	2	NA	NA	<0.05
24	0	0.2	ns	2	NA	NA	<0.05
24	0.05	0	ns	2	NA	NA	<0.05
24	0.05	0.05	ns	2	NA	NA	<0.05
24	0.05	0.1	ns	2	NA	NA	<0.05
24	0.05	0.15	ns	2	NA	NA	<0.05
24	0.05	0.2	ns	2	NA	NA	<0.05
24	0.1	0	ns	2	NA	NA	<0.05
24	0.1	0.05	ns	2	NA	NA	0.0956
24	0.1	0.1	ns	2	NA	NA	<0.05
24	0.1	0.15	ns	2	NA	NA	0.1381
24	0.1	0.2	ns	2	NA	NA	<0.05
24	0.15	0	ns	2	NA	NA	<0.05
24	0.15	0.05	ns	2	NA	NA	<0.05
24	0.15	0.1	ns	2	NA	NA	<0.05
24	0.15	0.15	ns	2	NA	NA	<0.05
24	0.15	0.2	ns	2	NA	NA	<0.05
24	0	0	s	2	NA	NA	0.7811
24	0	0.05	s	2	NA	NA	0.5788
24	0	0.1	s	2	NA	NA	0.2968
24	0	0.15	s	2	NA	NA	<0.05
24	0	0.2	s	2	NA	NA	0.0718
24	0.05	0	s	2	NA	NA	0.9179
24	0.05	0.05	s	2	NA	NA	0.4851
24	0.05	0.1	s	2	NA	NA	0.4465
24	0.05	0.15	s	2	NA	NA	<0.05
24	0.05	0.2	s	2	NA	NA	<0.05
24	0.1	0	s	2	NA	NA	0.6844
24	0.1	0.05	s	2	NA	NA	0.4627
24	0.1	0.1	s	2	NA	NA	0.1885
24	0.1	0.15	s	2	NA	NA	0.0597
24	0.1	0.2	s	2	NA	NA	<0.05
24	0.15	0	s	2	NA	NA	<0.6135
24	0.15	0.05	s	2	NA	NA	0.4104
24	0.15	0.1	s	2	NA	NA	<0.05
24	0.15	0.15	s	2	NA	NA	0.0557
24	0.15	0.2	s	2	NA	NA	<0.05

Table C4. Result of the beta regression models with dispersal as the predictor variable and BC dissimilarity as the response variable. *mean*±*sd*. Significance levels after Bonferroni correction: * 0.0025, ** 0.0005, *** 0.00005

Day	Factor	No stressor flux	Low stressor flux	Medium stressor flux	High stressor flux
8	Intercept	1.453 ± 0.209***	2.274 ± 0.276***	2.155 ± 0.233***	1.195 ± 0.324***
	BC diss	1.947 ± 0.235	-6.979 ± 1.977**	-9.317 ± 1.674***	-5.115 ± 2.455
12	Intercept	1.140 ± 0.289***	0.942 ± 0.294***	1.718 ± 0.190***	1.199 ± 0.196***
	BC diss	-9.086 ± 2.327**	-7.001 ± 2.364	-15.140 ± 1.537***	8.628 ± 1.510***
16	Intercept	1.338 ± 0.162***	0.767 ± 0.278**	0.923 ± 0.121***	1.044 ± 0.210***
	BC diss	-9.059 ± 1.267***	-11.433 ± 2.445***	-13.251 ± 1.084***	-12.215 ± 1.746***
20	Intercept	1.832 ± 0.316***	1.066 ± 0.272 ***	0.982 ± 0.244***	1.206 ± 0.341***
	BC diss	8.178 ± 2.343**	-5.739 ± 2.141**	-8.224 ± 2.011***	-7.725 ± 2.611
24	Intercept	2.536 ± 0.258***	1.672 ± 0.169***	0.758 ± 0.172***	0.548 ± 0.312
	BC diss	-15.555 ± 1.850 ***	-7.998 ± 1.263***	-7.743 ± 1.450***	-7.138 ± 2.683

Table C5. Results of the linear mixed model of the log transformed local density of *Navicula* sp. in the unexposed (left) and exposed (right) communities as response variable and dispersal, stressor flux, dispersal, time, time² and their interactions as predictor variables. Model selection was based on the backward selection protocol of Zuur 2009 using an ANOVA test. NA: predictor was removed during backward selection. Significance levels: * p<0.05, **p<0.01, ***<0.001.

	Unexposed community			Exposed community		
	Estimate	SD	t-value	Estimate	SD	t-value
Intercept	8.046	0.072	111.82	6.418	0.213	30.14***
Dispersal	0.153	0.557	0.27	2.681	1.740	-1.54
Stressor flux	0.740	0.793	0.93	-1.388	1.246	-1.11
Time	0.212	0.014	14.76***	0.138	0.026	5.21***
Time ²	-0.005	0.001	-6.45***	-0.003	0.001	-3.12**
dispersal x stressor flux	4.739	5.691	0.83	44.194	10.97	4.38***
Dispersal x time	0.163	0.098	1.67	-0.024	0.216	-0.111
Dispersal x time ²	-0.020	0.006	-3.40***	0.015	0.7	2.33*
Stressor flux x time	-0.556	0.126	-4.40***	0.172	0.069	2.51*
Stressor flux x time ²	0.018	0.008	2.37*	NA	NA	NA
Dispersal x stressor flux x time	NA	NA	NA	-2.299	0.560	-4.103***
Dispersal x stressor flux x time ²	0.085	0.029	2.99**	NA	NA	NA

Table C6. Results of the linear mixed model of the log transformed local density of *Navicula* sp. in the unexposed (left) and exposed (right) communities as response variable and dispersal, stressor flux, dispersal, time, time² and their interactions as predictor variables. Model selection was based on the backward selection protocol of Zuur 2009 using an ANOVA test. NA: predictor was removed during backward selection. Significance levels: * p<0.05, **p<0.01, ***<0.001.

	Unexposed community			Exposed community		
	Estimate	SD	t-value	Estimate	SD	t-value
Intercept	8.595	0.231	37.24***	8.401	0.084	99.90***
Dispersal	2.307	1.883	1.22	1.063	0.606	1.76
Stressor flux	6.447	2.812	2.29*	-0.482	0.873	-0.55
Time	0.166	0.035	4.76***	0.072	0.011	6.32***
Time ²	-0.007	0.001	-6.04***	-0.004	0.001	-5.82***
dispersal x stressor flux	-49.559	22.815	-2.17*	10.039	6.234	1.61
Dispersal x time	-0.443	0.285	-1.55	0.446	0.082	5.44***
Dispersal x time ²	0.015	0.010	1.57	-0.016	0.005	-3.06**
Stressor flux x time	-1.010	0.425	-2.58*			
Stressor flux x time ²	0.049	0.014	3.36***	0.022	0.004	6.19***
Dispersal x stressor flux x time	7.031	3.461	2.03*			
Dispersal x stressor flux x time ²	-0.231	0.118	-1.96	-0.087	0.026	-3.39***

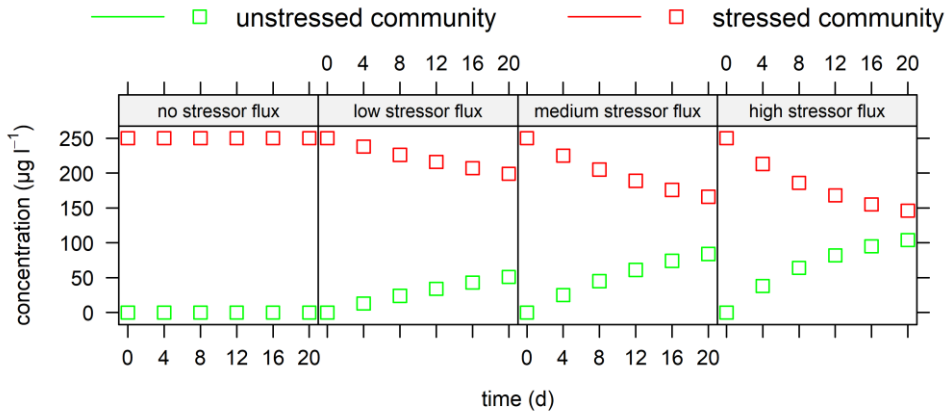


Fig. C1. Target concentration of atrazine in function of time for the unstressed and stressed community and for the different stressor flux levels. The symbols represent the concentration after the manipulation of the stressor flux on that day (see also Table C2a-C2c).

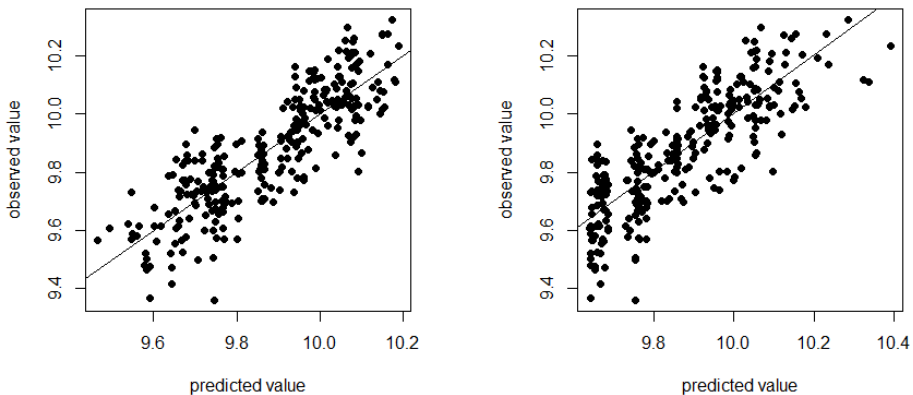


Fig. C2. Left: observed versus predicted plots of the linear mixed effect model with regional productivity as response variable and beta-diversity, stressor flux, dispersal, time, time² and their interactions as predictor variables. Right: observed versus predicted plots of the linear mixed effect model with regional productivity as response variable and beta-diversity, stressor flux, dispersal, time and their interactions as predictor variables.

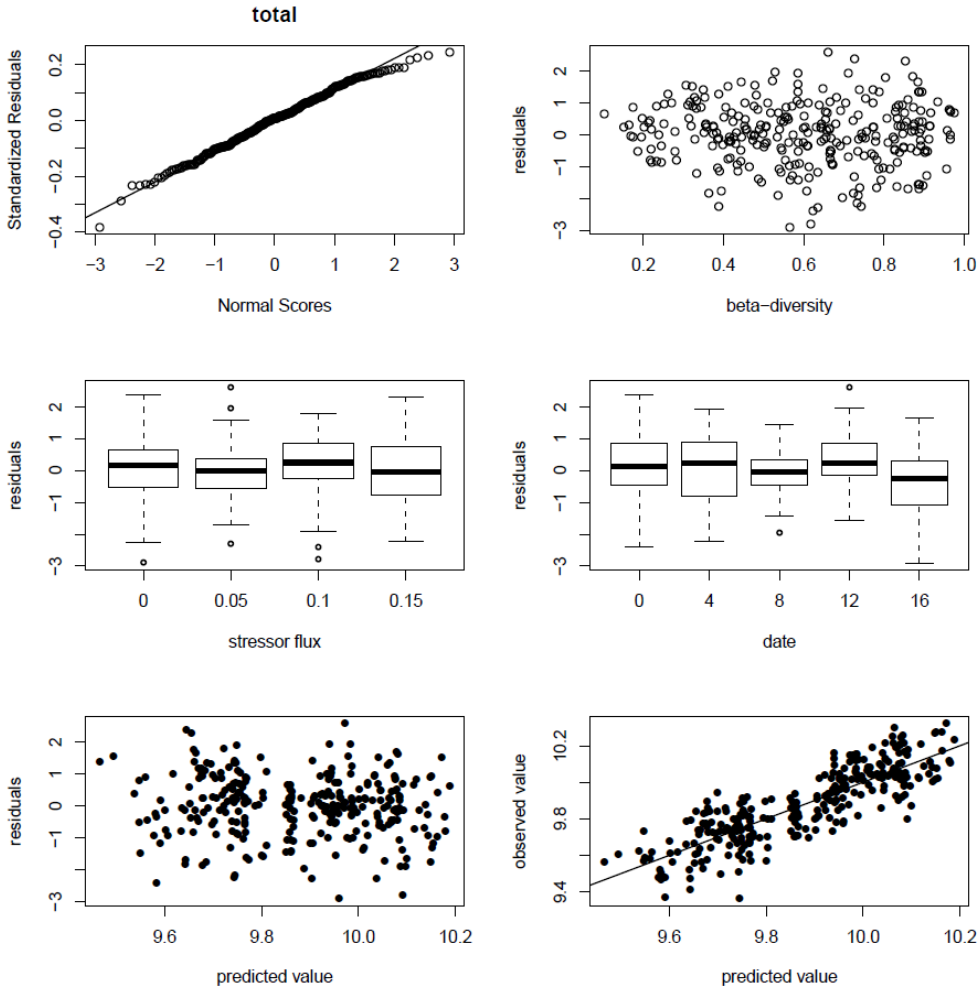


Fig. C3. Model validation of the linear mixed effect model with regional productivity as response variable and and beta-diversity, stressor flux, dispersal, time, time² and their interactions as predictor variables.

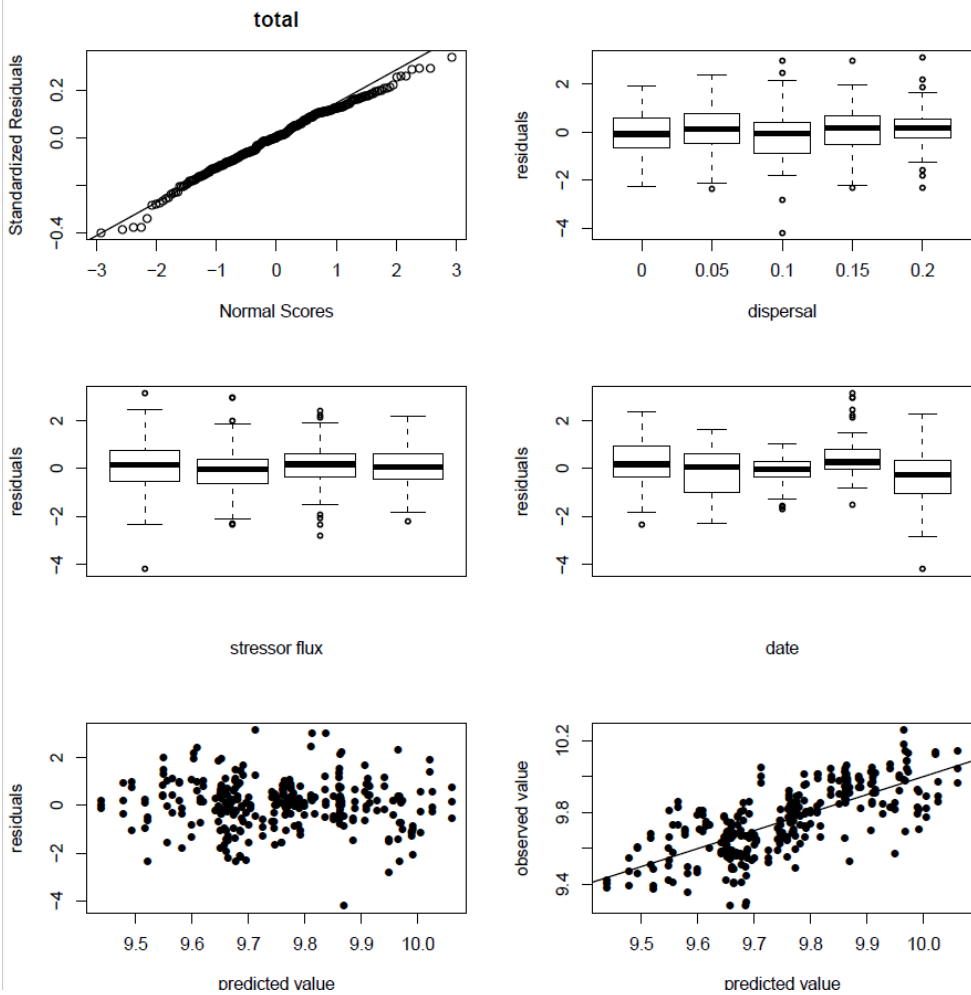


Fig. C4. Model validation of the linear mixed effect model with the local productivity in the unstressed community as the response variable and beta-diversity, stressor flux, dispersal, time, time² and their interactions as predictor variables.

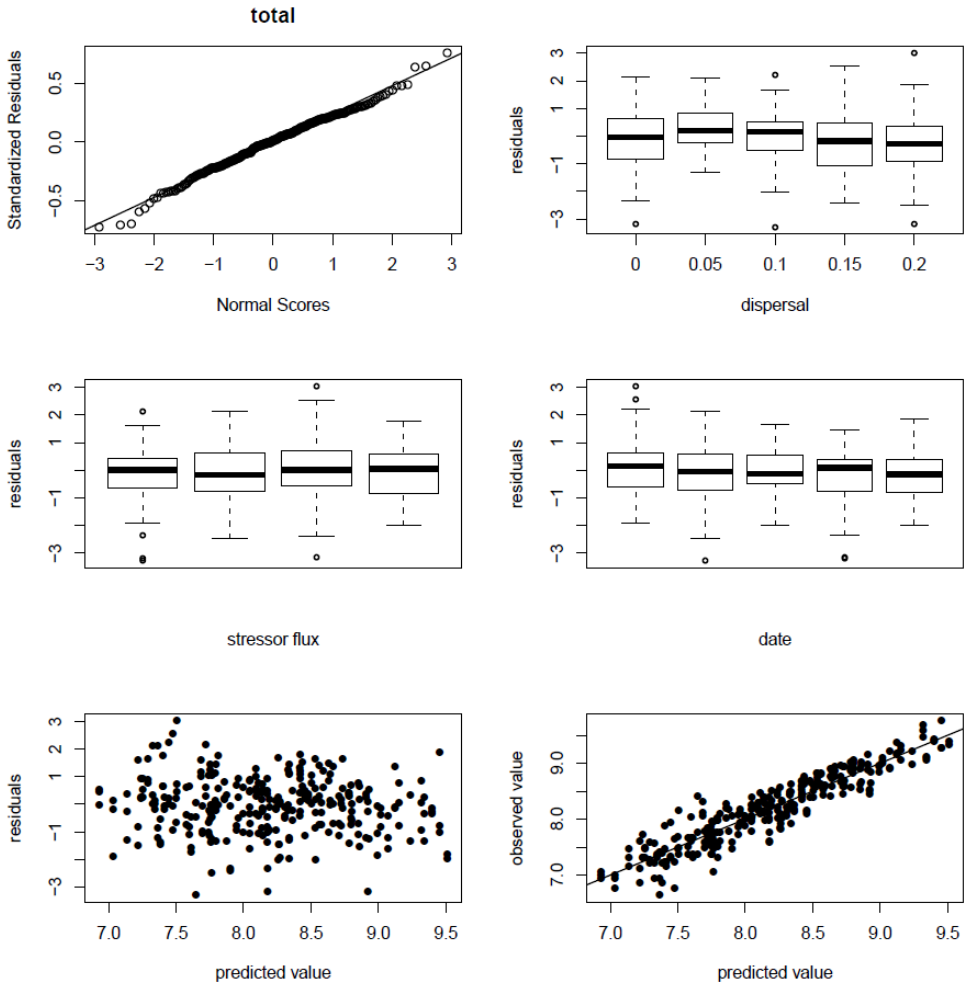


Fig. C5. Model validation of the linear mixed effect model with the local productivity in the stressed community as the response variable and beta-diversity, stressor flux, dispersal, time, time² and their interactions as predictor variables.

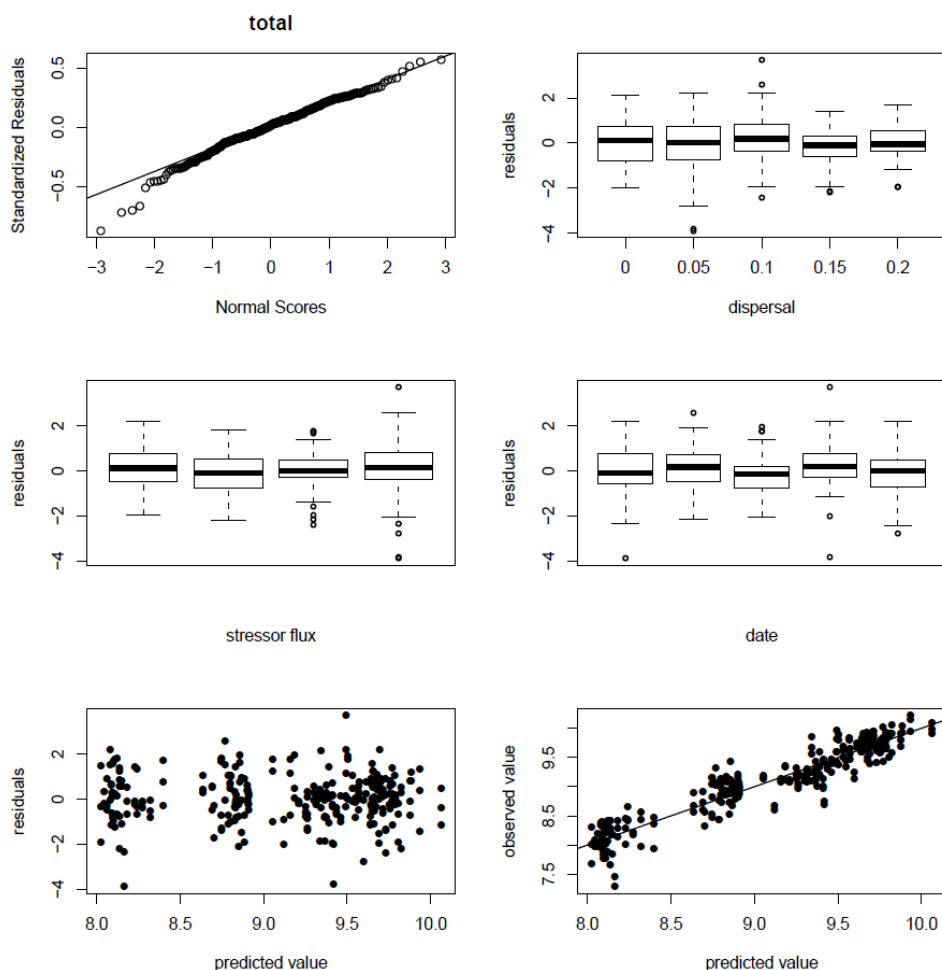


Fig. C6. Model validation of the linear mixed effect model with density of *Navicula* *sp.* in the unexposed community as the response variable and beta-diversity, stressor flux, dispersal, time, time² and their interactions as predictor variables.

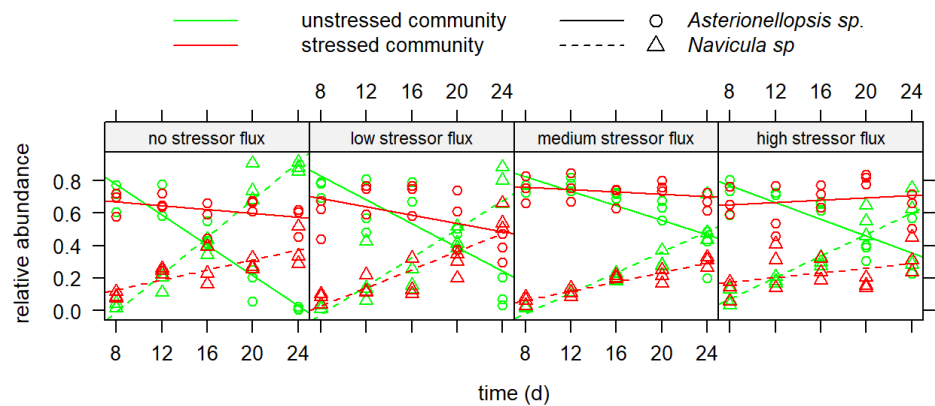


Fig. C7. The relative abundance of *Asterionellopsis sp.* and *Navicula sp.* in function of time in the no - dispersal treatments for the 4 stressor flux treatments. Symbols represent the data, the lines depict the best fit using a generalized linear model.

D

Supporting information for chapter 5

Appendix D. Tables and Figures.

Table D1. Species growth parameters in monoculture. Abbreviations: DACT: *Dactyliosolen* sp.; OD: *Odontella* sp.; μ : growth rate at 0 $\mu\text{g l}^{-1}$ of atrazine; K: carrying capacity at 0 $\mu\text{g l}^{-1}$; s : slope of the dose-response curve; $EC50$: effective concentration for 50% of the individuals. s and $EC50$ were determined using a three-parametric logistic function in the drc package.

species	μ (d^{-1})	K (μm^3)	s_{μ}	EC_{μ} ($\mu\text{g l}^{-1}$)	s_K	$EC50_{\mu}$ ($\mu\text{g l}^{-1}$)
DACT	0.19	3.4×10^9	12	116	23	148
OD	0.65	3.8×10^9	7	56	14	61

Table D2. Exposed and unexposed communities per replicate.

	Exposed communities	Unexposed communities
Replicate 1	1, 2, 6, 7	3, 4, 5, 8
Replicate 2	3, 4, 5, 8	1, 2, 6, 7
Replicate 3	1, 2, 4, 5	3, 6, 7, 8

Table D3. Connectivity matrices. The bold number represent the indices of the communities. “1” means that the according communities on the row and column are connected, “.” means unconnected.

24 connections								20 connections								16 connections										
	1	2	3	4	5	6	7	8		1	2	3	4	5	6	7	8		1	2	3	4	5	6	7	8
1	.	.	1	1	1	1	1	1	.	.	1	1	1	1	1	1	1	.	.	1	1	1	1	1	1	1
2	.	.	1	1	1	1	1	1	.	.	1	1	1	1	1	1	1	.	.	1	1	1	1	1	1	1
3	1	1	.	1	.	1	1	.	1	1	.	1	.	1	1	.	.	1	1	.	.	.	1	.	.	.
4	1	1	1	.	1	1	1	.	1	1	1	.	.	1	.	.	.	1	1	.	.	.	1	.	.	.
5	1	1	.	1	.	1	1	1	1	1	.	.	.	1	1	.	.	1	1	1	.	.
6	1	1	1	1	1	.	1	1	1	1	1	1	1	1	.	1	.	1	1	1	1	.	.	1	.	.
7	1	1	1	1	1	1	.	1	1	1	1	.	1	1	.	1	.	1	1	.	.	1	1	.	.	.
8	1	1	.	.	1	1	1	.	1	1	1	.	.	1	1

12 connections								8 connections								4 connections										
	1	2	3	4	5	6	7	8		1	2	3	4	5	6	7	8		1	2	3	4	5	6	7	8
1	.	.	1	1	1	1	.	1	.	.	1	.	1	1	.	1	1	1	.	.	.
2	.	.	1	1	.	1	1	1	.	.	1	1	.	1	1	.	.	.	1	.	.	1
3	1	1	1	1	1
4	1	1	1
5	1	1	.	1	1
6	1	1	1	.	1	1	1	1
7	.	1	.	.	1	1	.	.	.	1
8	1	1	1

Table D4. Model comparison using Log likelihood (LogLik) and Anova between the model with connectivity as a first-order predictor variable and the model with connectivity as a second-order predictor variable.

Day	Analysis using spatial correlation structure		
	LogLik first-order	LogLik second-order	p-value
12	567	570	0.15
30	937	937	0.78

Table D5. Results of the generalized linear model with connectivity, treatment, their interaction and start day as predictor variables and the log transformed regional relative density of *Dactylosolen* sp. as response variable.

	Day 12			Day 30		
	Value	SD	t-value	Value	SD	t-value
Intercept	0.008	0.001	7.15***	0.0002	0.0000	4.67***
Start day	-0.003	0.000	-7.58***	--0.0001	0.0000	-4.32***
atrazine app	0.001	0.001	0.88	0.0005	0.0002	2.47*
Connectivity	0.000	0.000	-0.308	0.0000	0.0000	2.45*
atrazine app x connectivity	0.000	0.000	-1.01	0.0000	0.0000	2.75**

Table D6. Results of the generalized linear model with connectivity, treatment, their interaction and start day as predictor variables and the log transformed relative density of *Dactylosolen* sp. in the unexposed and exposed communities as response variable.

	Day 12			Day 30		
	Value	SD	t-value	Value	SD	t-value
Intercept	0.0077	0.0008	10.03***	0.00021	0.00006	3.59***
Start day	-0.0037	0.0005	-6.74***	-0.00012	0.00003	-4.69***
Atrazine app.	0.0011	0.0012	0.90	-0.00026	0.00000	-1.21
Exposure	0.0017	0.0010	1.65	-0.00005	0.00008	-0.71
Connectivity	0.0000	0.0000	0.12	0.00000	0.00000	.014
Atrazine app x exposure	0.0068	0.0034	1.97*	0.01110	0.00298	3.73***
Atrazine app x connectivity	-0.0001	0.0001	-1.28	0.00005	0.00001	3.43***
Exposure x connectivity	-0.0001	0.00001	-1.17	0.00000	0.00000	0.957
Atrazine app x exposure x connectivity	-0.0002	0.0002	-1.26	-0.00035	0.00014	-2.56*

Table D7. Measured toxicant concentrations. Abbreviation: conc.: concentration

Connec- tivity	pat ch	exposure	measured conc. $\mu\text{g l}^{-1}$	Conne- tivity	pat ch	exposure	measured conc. $\mu\text{g l}^{-1}$
1	1	exposed	104	4	1	exposed	105
1	2	exposed	107	4	2	exposed	118
1	3	unexposed	10	4	3	unexposed	5
1	4	unexposed	11	4	4	unexposed	6
1	5	unexposed	10	4	5	unexposed	5
1	6	exposed	104	4	6	exposed	120
1	7	exposed	98	4	7	exposed	110
1	8	unexposed	13	4	8	unexposed	5
2	3	exposed	9	5	1	exposed	107
2	4	exposed	6	5	2	exposed	118
2	5	unexposed	7	5	3	unexposed	4
2	6	unexposed	115	5	4	unexposed	1
2	7	unexposed	105	5	5	unexposed	2
2	8	exposed	5	5	6	exposed	108
2	1	exposed	NA	5	7	exposed	131
2	2	unexposed	NA	5	8	unexposed	1
3	1	exposed	114	6	1	exposed	115
3	2	exposed	114	6	2	exposed	121
3	3	unexposed	7	6	3	unexposed	4
3	4	unexposed	7	6	4	unexposed	1
3	5	unexposed	7	6	5	unexposed	3
3	6	exposed	109	6	6	exposed	125
3	7	exposed	122	6	7	exposed	128
3	8	unexposed	4	6	8	unexposed	1

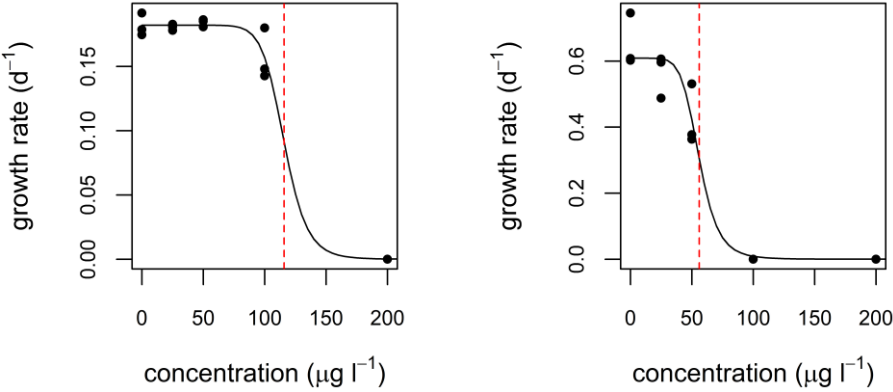


Fig. D1. Dose-response relationship on the growth rate of DACT (left) and OD (right).

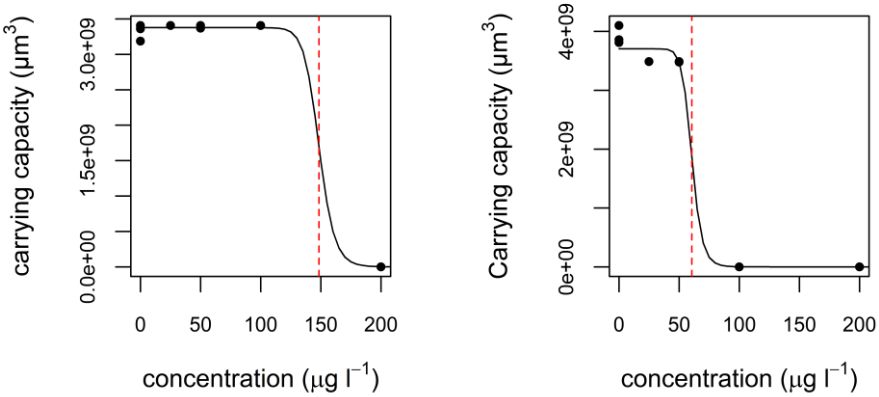


Fig. D2. Dose-response relationship on the carrying capacity of DACT (left) and OD (right).

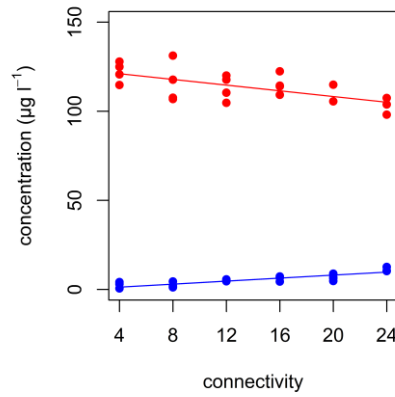


Fig. D3. Atrazine concentration in replicate 1 in function of connectivity. Each symbol represents the concentration in 1 patch. Blue: unexposed patches; red: exposed patches. Lines are the model predictions using a linear model with concentration as response variable and connectivity as predictor variable (connectivity: estimate = 0.423 ± 0.143 , $p=0.005$; connectivity x exposure: estimate = -1.221 ± 0.216 , $p<0.001$)

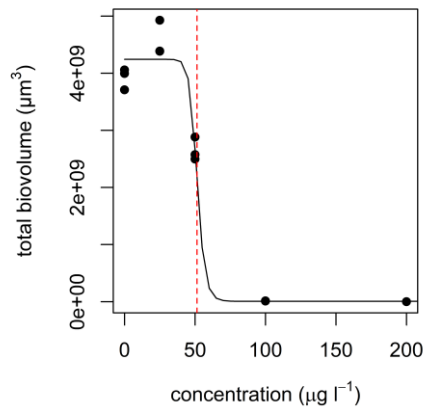


Fig. D4. Dose-response relationship of the total biovolume on day 30 in the isolated competition experiment. Parameters were determined using a four-parametric logistic function (Eq. 5.6). Parameter values: $b = 18$; $c = 5.8 \times 10^6$; $d = 1.2 \times 10^9$; $e = 51$.

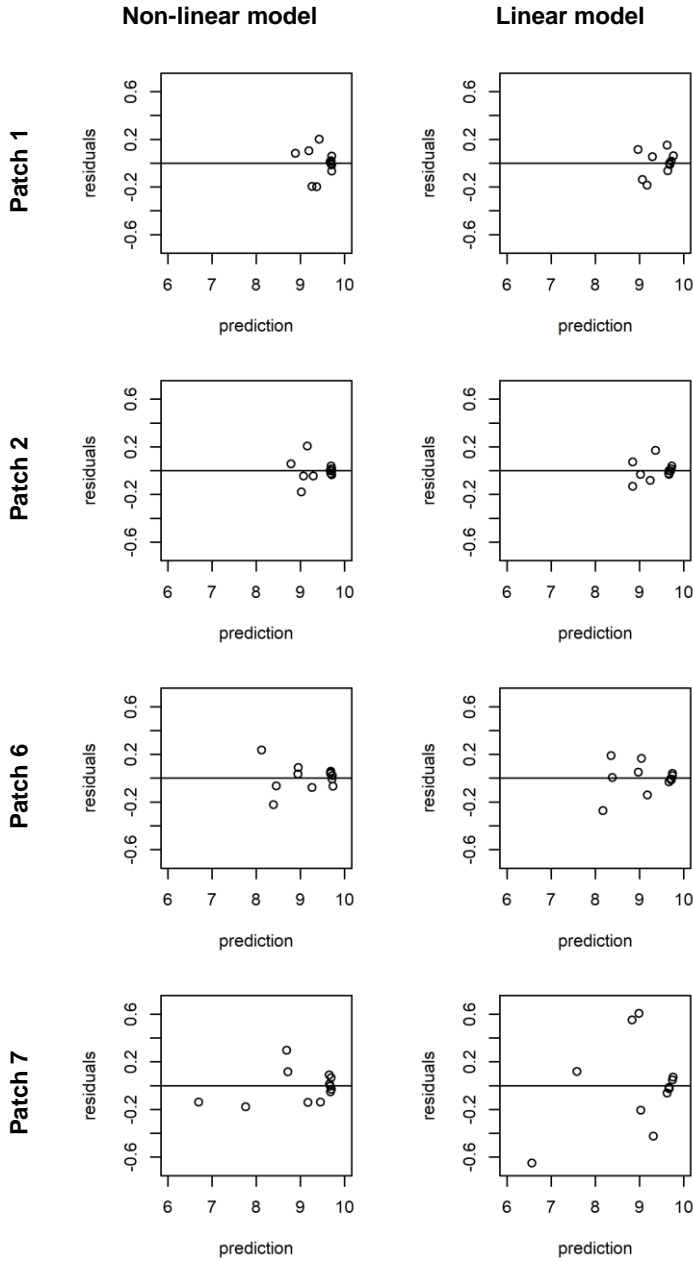


Fig. D5. Residuals in function of prediction for the non-linear models (left) and linear models (right) which predict the effect of treatment as a factor variable and local connectivity as continuous variable on the log transformed local productivity for patches 1, 2, 6 and 7 for replicate 1. The model on the left figure is given by Eq. 5.7. The left figure gives better model residuals for patch 7 by better predicting the productivity at the lowest local connectivity level.

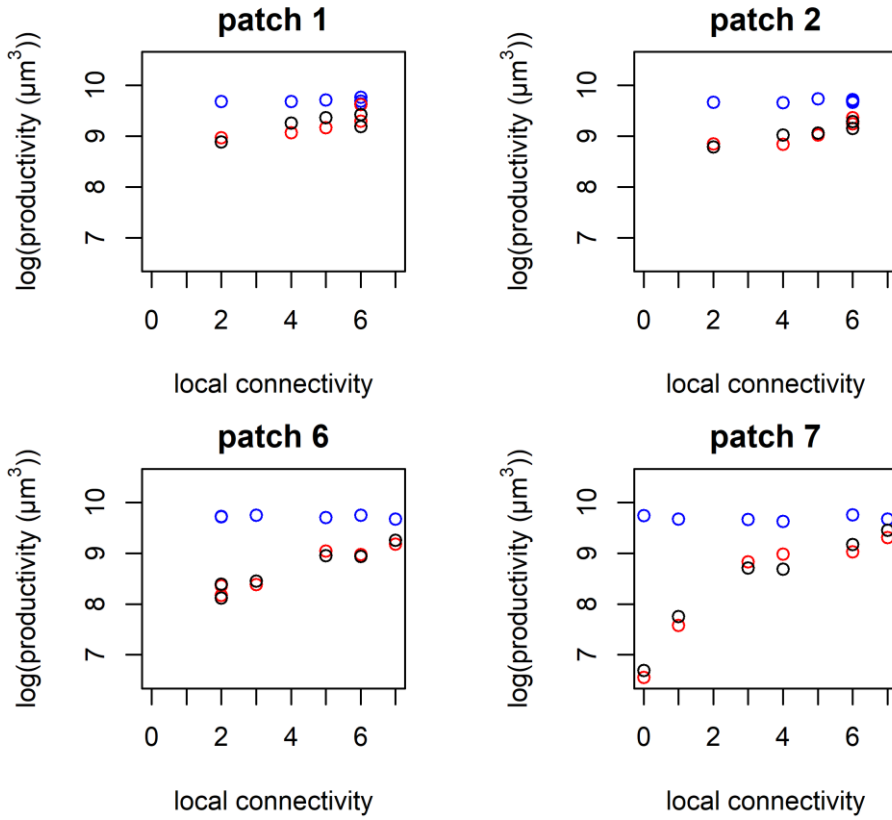


Fig. D6. log transformed local productivity in function of local connectivity for the patches 1, 2, 6 and 7 of replicate 1. Blue gives the exposed patches without atrazine application, red depicts the exposed patches with atrazine application. The black symbols represent the prediction of the data using Eq. 5.7.

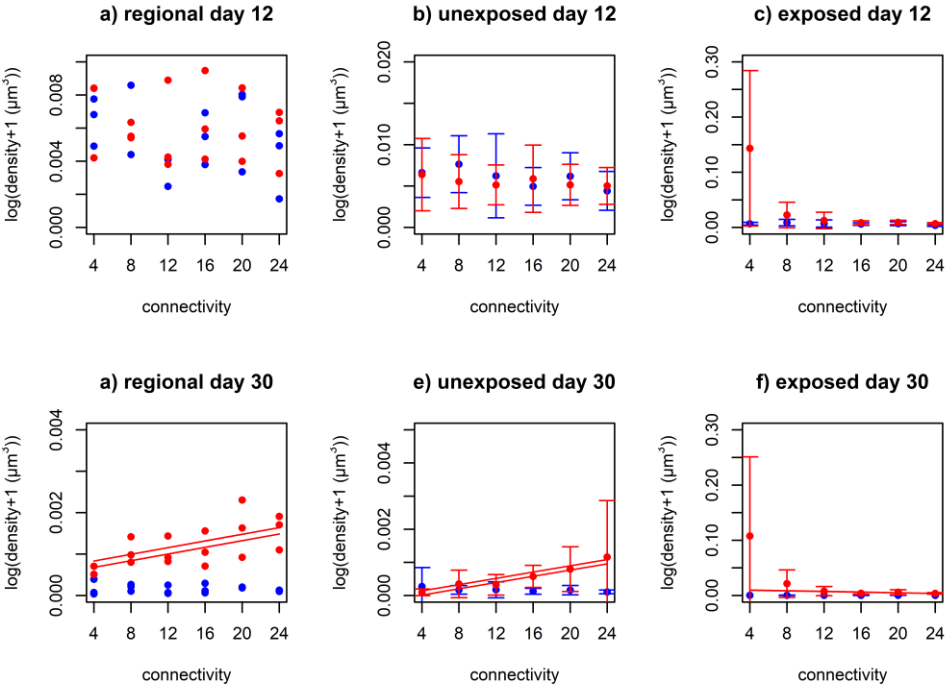


Fig. D7. The log transformed mean relative *density* of *Dactylosolen* sp. DACT in function of connectivity on days 12 and 30. Panels a and d represent the effect of connectivity on the relative abundance of DACT (mean \pm SD) in the control landscapes (blue) and the exposed landscapes (red). Panels b and e represent the effect of connectivity on the relative *density* of DACT (mean \pm SD) of the unexposed patches in the control landscape (blue) and the landscapes with atrazine application (red). Panels c and f represent the effect of connectivity on the relative *density* of DACT of the exposed patches in the control landscape (blue) and the landscapes with atrazine application (red). Symbols represent the data. The regression lines are determined using a generalized linear model and only shown when significant.

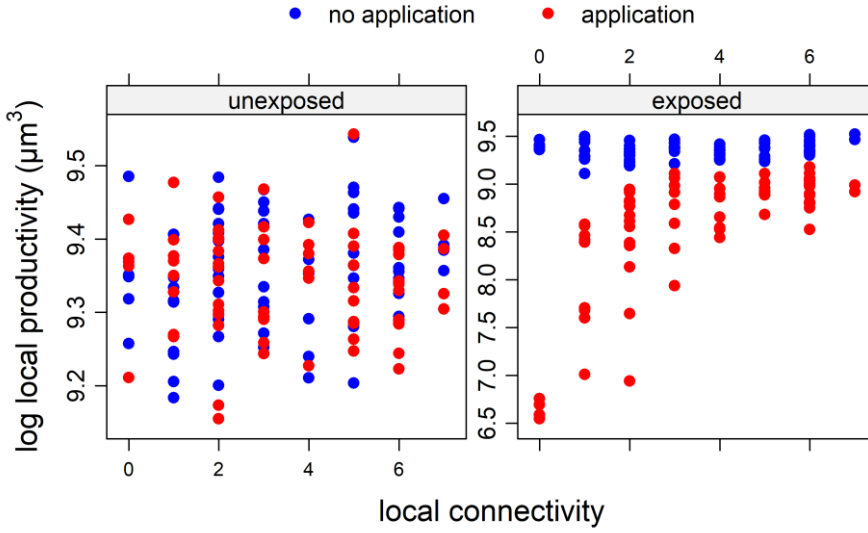


Fig. D8. Effect of local connectivity on log local productivity on day 12 in the unexposed and exposed communities for the treatment without atrazine application treatment (blue) and with atrazine application treatment (red).

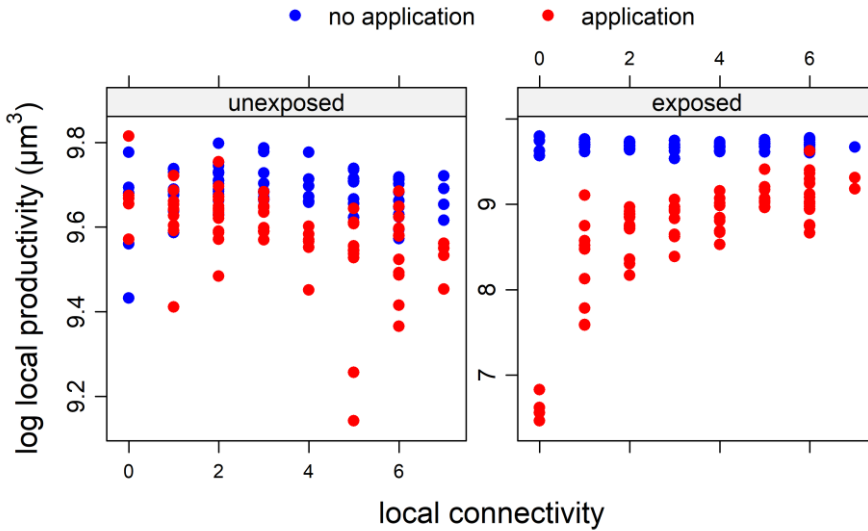


Fig. D9. Effect of local connectivity on log local productivity on day 30 in the unexposed and exposed communities for the treatment without atrazine application treatment (blue) and with atrazine application treatment (red).

Summary

Environmental change drivers, such as global warming and chemical pollution increasingly challenge the earth's ecosystems. Moreover, land use changes and habitat destruction fragment the landscape, which limits the movement of organisms between communities, named dispersal. How environmental changes and changes in dispersal rates combine in affecting biodiversity and productivity has only been addressed to a limited extent. In this dissertation, we therefore investigate the combined effect of environmental stress and dispersal on the diversity and productivity of micro-algae communities. To this end, we combine microcosm experiments (chapters 2, 4 and 5) and model simulations (chapter 3).

In **chapter 1**, we summarize how stress and dispersal may influence biodiversity and productivity. First, we give a general overview of how stressors can affect local community dynamics, leading to compositional and productivity changes. We then discuss how metacommunities, which are networks of communities connected by dispersal, can be used to investigate how regional processes interact with local dynamics. Next, we discuss which factors can change the relationship between dispersal and diversity and the relationship between dispersal and productivity. Finally, we motivate why the combined effect of stress and dispersal should be examined and discuss the research objectives of this thesis.

In **chapter 2**, we investigated how dispersal and the chemical stressor atrazine jointly affect the assembly, evenness and productivity of marine diatom communities. A priority effect regulated the assembly of the unstressed communities. However, in the high-stressed communities, the priority effect was small and community assembly was regulated by the selection of stress-tolerant species that replaced stress-sensitive species. Dispersal reduced evenness in the unstressed and stressed communities to a similar extent because the initial colonizers dominated the former, while the stress-tolerant species dominated the latter. Dispersal negatively affected biovolume in the unstressed communities because of high local competition. In contrast, dispersal increased productivity in the high-stressed communities by introducing stress-tolerant species, creating spatial insurance.

In chapter 2, the identity of the introduced species did not emerge from community processes. However, in reality, species move among communities, and the identity and the number of organisms that immigrate to a community depends on the composition and population size of the community from which the organisms emigrate. Stress heterogeneity is one factor that can create differences in composition and population size among communities. However, the extent to which stress heterogeneity creates different compositions depends on the interspecific variation in stress response. A second factor that creates differences in composition among communities is a heterogeneous starting composition. In **chapter 3**, we

therefore expanded the work done in chapter 2 by investigating if the relationship between dispersal and local diversity depends on stress heterogeneity. We used a metacommunity model to simulate the relationship between dispersal and diversity for 200 different metacommunities. We showed that the effect of dispersal on diversity depended on the magnitude of stress heterogeneity. The higher the stress heterogeneity, the stronger the difference in composition and population size among communities. As long as differences in population size were limited, stronger differences in composition increased the proportion of hump-shaped relationships between dispersal and diversity. However, when differences in composition and population density were high at a high stress heterogeneity, hump-shaped relationships only appeared in the communities with the highest stress-intensity. Instead, no hump-shaped relationships appeared in the communities with the lowest stress-intensity because the number of organisms that dispersed from the high-stressed communities was too small. The effect of stress heterogeneity on the proportion of hump-shaped relationships increased when the interspecific variation of the stress response increased. Moreover, when the starting composition was heterogeneous, more hump-shaped relationships appeared at a low stress heterogeneity than when the starting composition was homogeneous.

While only the dispersal of organisms was manipulated in chapters 2 and 3, also stressors can move among communities. The flux of a stressor might generate shifts in the environmental conditions, potentially changing how dispersal affects diversity and productivity, and as such the relationship between both. In **chapter 4**, we investigated how the flux of a chemical stressor influenced the relationship between among-community diversity and regional productivity. We addressed this question by manipulating dispersal and a stressor flux in two-patch metacommunity systems with micro-algae. We created stress heterogeneity by exposing one community to the chemical and manipulated among-community diversity by applying a dispersal gradient. The stressor flux shifted the relationship between among-community diversity and regional productivity from positive to negative. In absence of the stressor flux, a positive relationship appeared at the end of the experiment because dispersal decreased among-community diversity and regional productivity. Dispersal reduced regional productivity by removing organisms from their optimal community, disrupting local dynamics. In presence of the stressor flux, the relationship between among-community diversity and regional productivity was often negative as dispersal decreased among-community diversity but increased regional productivity. Dispersal increased productivity in the stressed community by increasing recovery when the concentration of the chemical decreased due to the stressor flux.

In chapters 3 and 4, we investigated the effect of stress and dispersal on local and regional diversity and productivity in two-patch metacommunities, and dispersal was manipulated by

applying different dispersal rates among communities. However, communities are typically embedded in spatially-connected landscapes. In such landscapes, chemical stressors are heterogeneously distributed among communities, changing the effect of connectivity on diversity and productivity. In **chapter 5**, we therefore investigated how a chemical stressor and connectivity affect the productivity and diversity in spatially-extended landscapes. Independent of the presence of the chemical stressor, connectivity did not affect regional productivity. However, in the landscapes exposed to a chemical stressor, connectivity affected local productivity by increasing the productivity of the exposed communities, while reducing the productivity of the unexposed communities to a similar extent. Connectivity did not affect regional diversity in the landscapes where the chemical stressor was absent but increased regional diversity in the landscapes with a chemical stressor present. Connectivity increased regional diversity because connectivity increased the relative abundance of the stress-tolerant species in the unexposed communities.

In **chapter 6** we discuss how environmental stress generates changes in composition and population size, which affect the relationship between dispersal and diversity. Moreover, we discuss the different ways in which dispersal can increase productivity in stressed communities. We further explain that a productivity increase in the stressed communities can have no effect on regional productivity, but can also increase or decrease regional productivity. We also add that a stressor flux may strongly change the effect of dispersal on local and regional productivity. Moreover, we discuss how connectivity in spatially-extended landscapes may affect diversity and productivity differently than when dispersal is manipulated in simple two-patch metacommunities. In chapter 6, we also formulate some research perspectives by pointing out that active movement of organisms and the presence of multiple trophic levels can strongly change dispersal effects on diversity and productivity. Last, we inspect potential consequences of the obtained results for the ecological risk assessment of chemicals.

Samenvatting

Factoren die de omgeving beïnvloeden, zoals klimaatsverandering en chemische vervuiling, stellen de ecosystemen op aarde steeds meer onder druk. Ons landschap is bovendien steeds meer versnipperd door veranderingen in het landgebruik en habitatvernietiging. Deze versnippering beperkt de beweging van organismen, genaamd dispersie, tussen gemeenschappen. Hoe omgevingsveranderingen en veranderingen in dispersie de biodiversiteit en productiviteit van gemeenschappen samen beïnvloeden is slechts in beperkte mate gekend. In deze thesis onderzoeken we daarom het gecombineerde effect van omgevingsstress en dispersie op de diversiteit en productiviteit van micro-algengemeenschappen. Daartoe combineren we experimenten (hoofdstukken 2, 4 en 5) en modelsimulaties (hoofdstuk 3).

In **hoofdstuk 1** vatten we samen hoe stress en dispersie de biodiversiteit en productiviteit van gemeenschappen kunnen beïnvloeden. Eerst geven we een algemeen overzicht van hoe stressoren de lokale gemeenschapsdynamiek kunnen beïnvloeden, wat leidt tot veranderingen in compositie en productiviteit. Vervolgens bespreken we hoe metagemeenschappen, netwerken van gemeenschappen die verbonden zijn door dispersie, kunnen worden gebruikt om te onderzoeken hoe regionale en lokale processen interageren. Vervolgens bespreken we welke factoren de relatie tussen dispersie en diversiteit en de relatie tussen dispersie en productiviteit kunnen veranderen. Ten slotte motiveren we waarom we het gecombineerde effect van stress en dispersie in deze thesis onderzochten en bespreken we de onderzoeksdoelstellingen van dit proefschrift.

In **hoofdstuk 2** onderzochten we hoe dispersie en de chemische stressor atrazine samen de samenstelling, gelijkmatigheid (*evenness*) en productiviteit van mariene diatomeeëngemeenschappen beïnvloeden. Een prioriteitseffect reguleerde de samenstelling van de niet-gestreste gemeenschappen. In de gestreste gemeenschappen was het prioriteitseffect klein en werd de gemeenschapssamenstelling gereguleerd door de selectie van stresstolerante soorten die de stressgevoelige soorten vervingen. Dispersie verminderde *evenness* in de niet-gestreste en gestreste gemeenschappen in een gelijke mate omdat de initiële soorten de niet-gestreste gemeenschappen domineerden, terwijl de stresstolerante soorten de gestreste gemeenschappen domineerden. Dispersie had een negatieve invloed op productiviteit in de niet-gestreste gemeenschappen vanwege de hoge lokale competitie. Daarentegen verhoogde dispersie de productiviteit door stresstolerante soorten te introduceren in de gestreste gemeenschappen, waardoor een "Spatial Insurance Effect" werd gecreëerd.

In hoofdstuk 2 werd de identiteit van de geïntroduceerde soorten niet beïnvloed door gemeenschapsprocessen. Echter, in werkelijkheid bewegen soorten zich tussen gemeenschappen, en de identiteit en het aantal organismen dat naar een gemeenschap migreert, hangt af van de samenstelling en productiviteit van de gemeenschap waaruit de organismen emigreren. Stress heterogeniteit creëert verschillen in samenstelling en populatiegroottes tussen gemeenschappen. De mate waarin stressheterogeniteit leidt tot verschillende samenstellingen, hangt echter af van de interspecifieke variatie in stressrespons. Een tweede factor die verschillen in samenstelling tussen gemeenschappen creëert, is een heterogene initiële soortensamenstelling. In **hoofdstuk 3** onderzochten we daarom hoe de relatie tussen dispersie en diversiteit afhangt van stressheterogeniteit. We gebruikten een metagemeenschapsmodel om de relatie tussen dispersie en diversiteit te simuleren voor 200 verschillende metagemeenschappen, die elk uit twee gemeenschappen bestonden. De simulaties toonden aan dat het effect van dispersie op diversiteit afhangt van de omvang van stress heterogeniteit. Hoe sterker de stress heterogeniteit, hoe groter het verschil in samenstelling en populatiegroottes tussen de gemeenschappen. Zolang de verschillen in de populatiegrootte klein waren, leidden sterkere verschillen in samenstelling tot een hoger aandeel aan unimodale relaties tussen dispersie en diversiteit. Wanneer verschillen in samenstelling en populatiegrootte groot waren bij een hoge stressheterogeniteit, verschenen uniforme relaties enkel in de gemeenschappen met de hoogste stressintensiteit. Daarentegen verschenen geen uniforme relaties in de gemeenschappen met de laagste stressintensiteit omdat het aantal organismen dat uit de meest-gestreste gemeenschap disperseerde te laag was. Het effect van stressheterogeniteit op het aandeel uniforme relaties nam toe wanneer de interspecifieke variatie van de stressrespons steeg. Bovendien verschenen meer uniforme relaties bij een lagere stressheterogeniteit wanneer de initiële gemeenschapssamenstelling heterogeen was dan wanneer deze homogeen was.

In hoofdstukken 2 en 3 werd enkel de dispersie van organismen tussen gemeenschappen gemanipuleerd. In werkelijkheid kunnen ook stressoren zich verplaatsen tussen gemeenschappen. Een stressor flux kan veranderingen in de omgevingscondities veroorzaken, en op deze manier het effect van dispersie op diversiteit en productiviteit beïnvloeden, en als zodanig de relatie tussen beide. In **hoofdstuk 4** onderzochten we daarom hoe een stressor flux de relatie tussen de diversiteit tussen gemeenschappen en regionale productiviteit beïnvloedde. Daarom manipuleerden we dispersie en een stressor flux tussen gemeenschappen van micro-algen. We creëerden stressheterogeniteit door een gemeenschap bloot te stellen aan een chemische stressor en manipuleerden de bèta-diversiteit (diversiteit tussen gemeenschappen) door een dispersie gradiënt toe te passen. De stressor flux wijzigde de relatie tussen bèta-diversiteit en regionale productiviteit van positief

naar negatief. Zonder stressor flux was er aan het einde van het experiment een positieve relatie omdat dispersie bèta-diversiteit en regionale productiviteit verkleinde. Dispersie verkleinde de regionale productiviteit door organismen uit hun meest geschikte gemeenschap te verwijderen en op deze manier de lokale dynamiek te verstoren. In aanwezigheid van de stressflux was de relatie tussen bèta-diversiteit en regionale productiviteit vaak negatief, omdat dispersie de diversiteit verlaagde maar de regionale productiviteit verhoogde. Dispersie verhoogde de productiviteit in de gestreste gemeenschap wanneer de concentratie van de chemische stof afnam als gevolg van de stressorflux.

In de hoofdstukken 3 en 4 onderzochten we het effect van stress en dispersie op de lokale en regionale diversiteit en productiviteit in metagemeenschappen die bestonden uit slechts 2 gemeenschappen, waarbij dispersie werd gemanipuleerd door verschillende dispersiesnelheden tussen gemeenschappen toe te passen. Gemeenschappen zijn echter typisch ingebed in ruimtelijk uitgestrekte landschappen. In dergelijke landschappen zijn chemische stressoren heterogeen verdeeld over de gemeenschappen. Deze stressoren kunnen het effect van connectiviteit op diversiteit en productiviteit veranderen. In **hoofdstuk 5** onderzochten we daarom hoe een chemische stressor en connectiviteit de productiviteit en diversiteit in ruimtelijk uitgestrekte landschappen beïnvloeden. Onafhankelijk van de aanwezigheid van de chemische stressor had connectiviteit geen invloed op de regionale productiviteit. In de landschappen die werden blootgesteld aan de chemische stressor, beïnvloedde connectiviteit de lokale productiviteit door de productiviteit van de blootgestelde gemeenschappen te verhogen, terwijl ze de productiviteit van de niet-blootgestelde gemeenschappen in vergelijkbare mate verlaagde. Connectiviteit had geen invloed op regionale productiviteit in de landschappen waar de chemische stressor afwezig was, maar verhoogde regionale diversiteit in de landschappen waar de chemische stressor aanwezig was. Connectiviteit verhoogde de regionale diversiteit omdat connectiviteit de relatieve abundantie van de stress-tolerante soorten in de niet-blootgestelde gemeenschappen verhoogde.

In **hoofdstuk 6** bespreken we hoe omgevingsstress veranderingen in gemeenschapssamenstelling en populatiegroottes genereert, en op die manier de relatie tussen dispersie en diversiteit kan beïnvloeden. Bovendien bespreken we de verschillende manieren waarop dispersie de productiviteit van gestreste gemeenschappen kan verhogen. We leggen ook uit dat een productiviteitsverhoging in de gestreste gemeenschappen onder bepaalde omstandigheden geen effect heeft op de regionale productiviteit, maar de regionale productiviteit eveneens kan verhogen of verlagen. We voegen ook toe dat een stressflux het effect van verspreiding op lokale en regionale productiviteit sterk kan veranderen. Bovendien bespreken we hoe connectiviteit in ruimtelijk uitgestrekte landschappen diversiteit en

productiviteit anders kan beïnvloeden dan wanneer dispersie wordt gemanipuleerd in eenvoudige metageenschappen. In hoofdstuk 6 formuleren we ook enkele onderzoeksperspectieven door erop te wijzen dat de actieve verplaatsing van organismen en de aanwezigheid van meerdere trofische niveaus het effect van dispersie op diversiteit en productiviteit sterk kunnen beïnvloeden. Ten slotte bekijken we mogelijke consequenties van de verkregen resultaten voor de ecologische risicobeoordeling van chemicaliën.

Curriculum Vitae

Personalia

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Education

2014-present	<p>Doctor in Applied Biological Sciences Faculty of Bioscience Engineering, Ghent University</p> <p>Doctor in Sciences Faculty of Sciences, University of Namur</p> <p>Thesis: "The combined effect of dispersal and chemical stress on the diversity and productivity of marine micro-algae communities"</p>
2012-2014	Master of Science in Bioscience Engineering: Environmental Technology (Greatest distinction), Ghent University
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Employment

01/10/2014-30/09/2018	PhD research Fellow FWO (Research Foundation Flanders) at the Laboratory of Environmental Toxicology and Aquatic Ecology, Ghent University - GhEnToxLab
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Publications

Peer-reviewed articles (A1)

De Raedt J., Baert J.M., Janssen C.R., De Laender F. 2019. Stressor fluxes alter the relationship between beta-diversity and regional productivity. *Oikos*. *In press*.

De Raedt J., Baert J.M., Janssen C.R., De Laender F. 2017. Non-additive effects of dispersal and selective stress on structure, evenness, and biovolume production in marine diatom communities. *Hydrobiologia* 788: 385-396.

Radchuk, V., De Laender, F., Cabral, Sarmiento J., Boulangeat I, Crawford M., Bohn F., **De Raedt J.**, Scherer C., Svenning JC, Thonicke K, Schurr F.M., Grimm V, Kramer-Schadt S. 2019. Ecology Letters. The dimensionality of stability depends on disturbance type. *In press*.

Fronhofer E., Legrand D., Altermatt F., Anstätt A., Blanchet S., Bonte D., Chaine A., Dahirel M., De Laender F., **De Raedt J.**, Di Gesù L., Jacob S., Kaltz O., Laurent E., Little C., Madec L., Manzi F., Masier S., Pellerin F., Pennekamp F., Schtickzelle N., Therry L., Vong A., Winandy L., and Côté J. 2018. Bottom-up and top-down control of dispersal across major organismal groups. *Nature Ecology and Evolution* 2: 1859-1863.

Platform presentations

De Raedt J., De Laender F., Baert J.M., Janssen C. R. "The effect of connectivity on productivity and diversity in micro-algae communities". VLIZ Marine Science Day, Bredene, Belgium, 21 March 2018.

De Raedt J., Janssen C.R., Baert J.M., De Laender F. "The relationship between regional diversity and productivity over a stress dispersal gradient". FAME conference, Ghent, Belgium, 1 December 2016.

Poster presentations

De Raedt J., Janssen C.R., Baert J.M., De Laender F. "Toxicant movement changes the relationship between regional diversity and productivity". SETAC (Society of Environmental toxicology and Chemistry) Conference, Brussels, Belgium, 8 May 2017.

De Raedt J., Janssen C.R., Baert J.M., De Laender F. "Movement of chemical stressors changes the relationship between regional diversity and productivity". VLIZ (Vlaams Instituut voor de Zee) Marine Science Day, Bruges, Belgium, 3 March 2017.

De Raedt J., De Laender F., Baert J.M., Janssen C.R. "Algal and toxicant dispersal are key factors for maintaining biovolume production in diatom communities affected by a toxic stressor". VLIZ Marine Science Day, Bruges, Belgium, 12 February 2016.

De Raedt J., Baert J.M., Janssen C.R., De Laender F. "The effect of dispersal along a stress gradient in micro-algae communities". ESA (Ecological Society of America) Conference, Baltimore, USA, 10 August 2015.

De Raedt J., Baert J.M., Janssen C.R., De Laender F. "Does habitat connectivity reduce the amount of stress-tolerance variability needed to preserve ecosystem functions?". SETAC Conference, Barcelona, Spain, 5 May 2015.

De Raedt J., Baert J.M., De Laender F., Janssen C.R. "Interactions between chemical stress and dispersal". SETAC Conference, Barcelona, Spain, 5 May 2015.

De Raedt J., Baert J.M., De Laender F., Janssen C.R. "Interaction between chemical stress and dispersal in marine phytoplankton communities". VLIZ Marine Science Day, Bruges, Belgium, 20 February 2015.

Involvement

Member of the Faculty Board of the Faculty of Bioscience Engineering. October 2012 until September 2014.

Member of the Educational Commission Master of Science in Bioscience Engineering: Environmental Technology. October 2016 until September 2018.

Tutor of Master thesis of Irene Govaert. Thesis: Het gecombineerde effect van actieve dispersie en chemische stress en co-existentie. Master of Science, Industrial Sciences: Biochemistry. 2016-2017. Promotors: Colin R. Janssen, Frederik De Laender.